THE JOURNAL OF WILDLIFE MANAGEMENT

U. OF N. MAY 6 1957 FORESTRY LIBRARY

APRIL - 1957
Vol. 21 No. 2

CONTENTS

THE CAUSALITY OF MICROTINE CYCLES IN GERMANY — *Fritz Frank* 113

RESPONSES OF FORAGE TO TIMBER STAND IMPROVEMENT IN THE MISSOURI OZARKS — *Thomas S. Baskett, Robert L. Dunkeson and S. Clark Martin* 121

REPRODUCTION OF CARP, LARGEMOUTH BASS, BLUEGILLS AND BLACK CRAPPIES IN SMALL REARING PONDS — *Donald Mraz and Edwin L. Cooper* 127

NOTES ON TOOTH DEVELOPMENT AND WEAR FOR ROCKY MOUNTAIN MULE DEER — *W. Leslie Robinette, Dale A. Jones, Glenn Rogers and Jay S. Gashwiler* 134

A SUMMER WHISTLING COCK COUNT OF BOBWHITE QUAIL AS AN INDEX TO WINTERING POPULATIONS — *Walter Rosene, Jr.* 153

RANGE USE, FOOD HABITS, AND AGRICULTURAL RELATIONSHIPS OF THE MULE DEER, BRIDGER MOUNTAINS, MONTANA — *Bruce T. Wilkins* 159

WEIGHT AND BODY-FAT RELATIONSHIPS OF MOURNING DOVES IN ILLINOIS — *Harold C. Hanson and Charles W. Kossack* 169

CONCLUSIONS FROM A TEN-YEAR CREEL CENSUS ON A LAKE WITH NO ANGLING RESTRICTIONS — *Warren Churchill* 182

MULE DEER AND ELK FOOD HABITS ON THE NATIONAL BISON RANGE — *Melvin S. Morris and John E. Schwartz* 189

RELATION OF HAY HARVESTING TO DUCK NESTING UNDER A REFUGE-PERMITTEE SYSTEM — *Ronald F. Labisky* 194

GALVANOTAXIC RESPONSE OF FISH TO PULSATING DIRECT CURRENT — *Glenn N. Taylor, Larry S. Cole and William F. Sigler* 201

NICOTINE SALICYLATE FOR CAPTURING DEER — *Jack A. Crockford, Frank A. Hayes, James H. Jenkins and Seldon F. Feurt* 213

A BRIEF ACCOUNT OF THE DEER IN AUSTRALIA — *Arthur Bentley* 221

A TECHNIQUE FOR SAMPLING MOURNING DOVE PRODUCTION — *J. F. Jumber, H. O. Hartley, E. L. Kozicky and A. M. Johnson* 226

ANIMAL CYCLES AND FOOD — *J. Burton Lauckhart* 230

OBITUARY: NATHAN WARREN FELLOWS, JR. 234

BRIEFER ARTICLES

FOOD OF WOOD DUCKS — *Malcolm W. Coulter* 235

FOOD OF FUR SEALS IN THE EASTERN BERING SEA — *Ford Wilke and Karl W. Kenyon* 237

DISPHARYNX NASUTA IN HUNGARIAN PARTRIDGE IN ONTARIO — *J. F. Bendell and R. D. Lisk* 238

STRESS RESPONSE AND SURVIVAL TIME IN THREE WILDLIFE SPECIES — *Ruth L. Hine and Kenneth G. Flakas* 239

FOOD OF SEA OTTERS AND HARBOR SEALS AT AMCHITKA ISLAND — *Ford Wilke* 241

SOCIAL AND RANGE DOMINANCE IN GALLINACEOUS BIRDS—PHEASANTS AND PRAIRIE GROUSE — *Ward M. Sharp* 242

A MARSH DEER "DIE-OFF" IN LOUISIANA — *Leslie L. Glasgow and Allan Ensminger* 245

CROP THICKENING AND SEPTEMBER NESTING OF DOVES — *Larry D. Caldwell* 247

VALIDITY OF SPUR LENGTH AS AN AGE CRITERION IN PHEASANTS — *Allen W. Stokes* 248

A COLLAR FOR IDENTIFICATION OF BIG GAME — *Donald R. Progulske* 251

REVIEWS 253

The Journal of Wildlife Management is published by The Wildlife Society in January, April, July and October. Subscription $6.00 per year and current numbers $1.50. Society members cover subscription in annual dues. Back issues are available at $8.00 per volume, $2.00 per issue except the following, which are out of print: Vol. 1, Nos. 1, 2 & 3; Vol. 2, Nos. 2, 3 & 4; Vol. 3, all issues; Vol. 5, Nos. 3 & 4; Vol. 7, Nos. 1, 2 & 4; and Vol. 8, Nos. 1, 2 & 3.

Manuscripts for publication, books and papers for review, news notes and correspondence concerning them should be sent to the *Editor*, JOSEPH J. HICKEY, 424 University Farm Place, Madison 5, Wisconsin.

Dues, subscriptions, changes of address, requests for missing numbers, applications for membership, and other correspondence should be sent to the *Executive Secretary*, DANIEL L. LEEDY, Branch of Wildlife Research, U. S. Fish and Wildlife Service, Washington 25, D.C.

The Society is not responsible for supplying missing issues unless the Executive Secretary is notified within 60 days of the date of publication.

Entered as Second Class Matter, at the Post Office at Lawrence, Kansas, under the Act of March 3, 1879.

113
121
127
134
153
159
169
182
189
194
201
213
221
226
230
234
235
237
238
239
241
242
245
247
248
251
253

July
sub-
t the
sues;

con-
on 5,

nber-
anch

tified

March

THE JOURNAL OF WILDLIFE MANAGEMENT

VOLUME 21 APRIL 1957 NUMBER 2

THE CAUSALITY OF MICROTINE CYCLES IN GERMANY

(Second Preliminary Research Report)

Fritz Frank

Institut für Grünlandfragen der Biologischen Bundesanstalt für Land– und Forstwirtschaft, Philosophenweg 16, Oldenburg (Oldb), Germany

Hitherto the phenomenon of cycles has not been a subject of detailed research in central Europe, so one could have the impression that cycles of extreme degree do not exist in the temperate zones of this continent (and this is often asserted, indeed); but this is not the case. The central European rodents not only exhibit irregular population fluctuations, but some of them also show regular cycles of an intensity and a strict periodicity not inferior to those of the cyclic animals in the arctic zone. Primarily, there are large plague districts of *Microtus arvalis* Pallas in Germany and her neighbouring countries which can be followed back at least to the fifteenth century. Recently, these plague districts have increased because of cultivation measures, especially the drainage of moist lowlands and fens, which create optimal biotopes for the voles (Frank, 1953c, 1955, 1956b). Besides, particularly since the end of the last war, *Microtus agrestis* L. caused heavy damage in the forest plantations, as it did in Great Britain, and it did so in a decidedly cyclic manner (Frank, 1952). Systematic research on the causality of these cycles was started by the author in 1951 at first with main emphasis on *M. arvalis*. Besides detailed publications, a first preliminary report was given in 1954 (Frank, 1954b). In the meantime, many new results have been collected—in laboratory populations of more than 10,000 animals and in outdoor-cage populations, as well as in wild populations involving 1,150 individually marked animals. This paper summarizes the present state of the work, including as-yet-unpublished material. I am much indebted to Frances Hamerstrom, Plainfield (Wis.), and to Robert Rausch, Anchorage (Alaska) for critically revising my English rough copy, and also for inducing me to adjust my ecological terms to American usage and to formulate some passages more precisely.

The main emphasis on cyclic work formerly was mostly placed on the attempt to get to the bottom of the causality of cycles by analysing and explaining the periodicity from phenological data, often with speculation on cosmic causalities before having explored all terrestrial events and influences. In contrast, the German researches were concentrated on the observation and analysis of the internal events occurring in cyclic populations and on the environmental factors influencing them. Naturally, we are not able to solve all problems connected with microtine cycles in so short a time, but I dare say many partial solutions have now been attained. When assembled, they already show a rough picture of the cyclic structure established on a foundation of facts containing few elements of a speculative or hypothetical nature. In this way the cyclic phenomenon presents itself—as do other biological problems—as an interaction between biological events and environmental factors of a particularly complicated structure, depending on several factor-groups and many individual factors.

POPULATION INCREASE

First, population increase results from three factor-groups—the "reproductive potential" of the cyclic species, the "carrying capacity" of the environment, and that which I call in German "Verdichtungspotential" (Frank, 1954b), in English "condensation potential" of the cyclic species.

Reproductive Potential

This first factor-group is based on age at maturity, litter size, litter succession, and length of the reproductive season. Working

with a captive population of more than 10,000 laboratory-reared animals (Frank, 1956a) and individually marked wild populations of *M. arvalis* (yet unpublished), my findings concerning this point had most remarkable results. *M. arvalis* distinguishes itself by having a pronounced suckling-maturity. The young females, which suckle until the seventeenth day, already show a perforated vagina from the eleventh day on and are mated by old males from the thirteenth day on. Correspondingly, the earliest litters were dropped by a wild female 33 days old and by a captive female 34 days old (pregnancy lasts 19-21 days, on an average 20 days). Indeed under natural conditions, a high proportion of the young females mate in the maternal home range before being weaned or immediately after being weaned.[1] But this happens only in the spring and summer; the females born during and after September for the most part do not reach sexual maturity in the same year. In the autumn the young generally show a slower growth rate than in the spring and summer, when an astonishing growth rate is evident. At the age of about 40 days a pregnant female can weigh up to 34g., and the males of this age also may be as heavy as very old animals. Every analysis of vole populations for age classification based on weight classification, therefore, must lead to serious errors, and conclusions based on them are subject to question (Frank and Zimmerman, 1957).

Besides age at maturity, reproductive potential is based on litter size and litter succession. Litter size depends upon inheritance, upon age and size of the female, and upon season (Frank, 1956a), and is modified by several environmental influences; in particular, quality and quantity of food are of decisive importance. In *M. arvalis* maximum litter size is 12; in one case Reichstein (1957) found 13 embryos. Under optimal conditions postpartum mating is usual, so that one litter follows another every 20 days. The maximum number of litters produced by one female in my laboratory-reared population of more than 10,000 animals has been 33, with 127 young and an average litter size of 3.85. Under optimal food and climatic conditions in spring and summer, the average litter size in wild populations can amount to 7 young. Concerning reproductive efficiency, *M. arvalis* represents a maximum among all mammals hitherto investigated. In captive females the litter weight amounts to 53.2 per cent of the mother's weight (both measured immediately after birth), while in other mammals, for instance some other rodents and pygmy dogs, it is only one-third (Frank, 1956a).

Length of the reproductive season, a further factor influencing reproductive potential, continues from February or March to October or November, but under favourable conditions, for example in cornricks, reproduction goes on through the winter (Stein, 1953a; Frank, 1954b). On the whole, *M. arvalis*, and probably *M. agrestis*, both showing pronounced cycles, possess an uncommon reproductive potential attainable under the optimal environmental conditions presented in the plague districts.

Carrying Capacity of Environment

Whether or not this high reproductive potential causes a violent population increase depends on the second factor-group, the carrying capacity of the environment. In other words, it depends on whether or not the environment can support a high population. The individual factors influencing this are especially food, cover, sunlight, good overwintering places, and ground-water level (but in the case of *M. arvalis* not the nature and humidity of the soil). Also it is striking that all plague districts of *M. arvalis*, although they lie in very different geological formations (lowlands, marshes, fens, loam steppes, lower mountain regions, etc.), show very similar characteristics in the structure of their landscape. They always represent large, open, monotonous, and uniform biotopes with extremely scant cover of trees and bushes, which we call "cultivation steppes" caused by human activity in the once-wooded or marshy central European country. Extremely severe and regular plagues of *M. arvalis* occur only in such biotopes, evidently representing the ecological optimum for this species; in districts miscellaneously covered by varied biotopes

[1]Early maturity of females seems to be a general feature of the genus *Microtus* because I found mating females 20 days old also in *M. oeconomus* (Frank and Zimmermann, 1956). As far as I know suckling-maturity among other mammals has hitherto been established only for *Mustela erminea* L. (Müller, 1954).

and higher proportions of woods, trees, and bushes, only moderate fluctuations are visible. Doubtless these circumstances represent certain parallels to the opinion of Dymond (1947), that the uniformity of the arctic biotopes favours the amplitude of cycles. This further shows that not only the climate but also the structure of environment is important for the origin of regular cycles, which indeed are observable in the temperate zones where there are corresponding environmental conditions. The abundance and the cycles of *M. arvalis* are also influenced by the economic use of the country. Extensive agricultural use favours plagues, intensive use prevents plagues. On grazing land a low stock of cattle and an extensive pasturing favours plagues, while high stocks of cattle and intensive pasturing prevent plagues (Frank, 1956b).

Thus, in central Europe, the cycles of *M. arvalis* are "released" by human cultivation. This enables us to stop the development of plagues by an ecological and economic reorganisation of the plague districts. Based on this example the author has postulated the introduction of the more effective "ecological plague control" for crop protection, rather than the usual chemical pest control by poisons and biological control by encouragement of enemies and parasites (Frank, 1956b). In principle, the same is valid for *M. agrestis,* which shows regular fluctuations only in former woodland where the trees have been felled or new plantations of trees are laid out, and the bare plains are covered with large grass jungles, evidently representing the ecological optimum for this species (Frank, 1952, 1954b). In any case true cycles appear only under optimal environmental conditions permitting both the realization of the high reproductive potential and the establishment of the descendants produced by this potential: in other words, where a high carrying capacity is present. On this point our conclusions probably come near to some of the ideas expressed by Paul Errington.

Condensation Potential

The degree of the population increase depends decisively on the third factor-group: the condensation potential, which consists of certain behaviour mechanisms that enable many cyclic species to live at an uncommonly high population density. Before describing these behaviour mechanisms I must explain the new term "condensation potential" (Frank, 1954b). It is based on all intraspecific and especially social behaviour that favours the increase of density. Normally the condensation potential is limited by intrinsic behaviour, especially by territoriality, to a "saturation point" which is approximately adapted to the carrying capacity of the environment. It seems to be a feature of many cyclic species that they show particular social behaviour that abolishes the normal limits, and enables them, under optimal environmental conditions, to exceed the saturation point so far that the carrying capacity of the environment is greatly exceeded, and simultaneously population regulation by crash, mass emigration, or other drastic mechanisms becomes necessary and inevitable. In *M. arvalis* the condensation potential concerns: reduction of the home ranges, social communities of the females, and diminution or elimination of males. These points seem worth stressing as aspects of cycle research that further the understanding of this phenomenon and of population dynamics in general (Frank, 1954b, 1956a).

Fundamentally the European microtines are territorial animals; this we have demonstrated in the laboratory (Frank, 1953a, 1956a) as well as in individually marked wild populations. Females occupy a range around their burrows where they tolerate no stranger of their species. Females tolerate a strange male in their home ranges only when they are in heat and even then the male must fight to approach. With the exception of the short period of heat, all strangers of either sex are driven away. This home range has a diameter of 10-20 meters during the reproductive season. Males inhabit an irregular larger range, wandering from female to female to mate those that are in heat. They are only intolerant of strange males of mature age. Recently we found that in spring and summer the young males without exception disappear from their mother's territory and its surroundings after becoming mature, and the old males mating the resident females are all strangers, having immigrated from other places. This would tend to prevent inbreeding. In contrast, the young females settle in the immediate vicinity of their mother's home range, or sometimes within it. When space becomes scarce,

the size of the home ranges can be reduced. This also gives the voles a considerable condensation potential (Frank, 1953a).

In contrast to the territorial behaviour that causes intraspecific demarcation and guarantees the individual space and food needed for life and reproduction, the following mechanisms favour life in social communities and also high density. In the first place we have the "mother-family," consisting of the female and her suckling young, sometimes also her unmated subadult offspring. But this is not typical of spring and summer when, for the most part, the weaned young, particularly the males, leave the maternal home range. "Great families" arise every autumn, for the last two to three litters of the year remain in the maternal home range (because the female does not drive them out), and constitute the overwintering community (Frank, 1954a). This lightens existence in the cold season when stress is great; all live together in a single, thickly lined nest, the many small individuals form a greater thermal unit, and the loss of heat and energy is significantly reduced. Freezing weather and heavy precipitation reduce the activity of the voles, which remain in their nests and eat the food stores they have brought in during autumn. Nevertheless, the size of the home ranges and the radius of activity of the voles is importantly enlarged during winter (about four or five times larger than the summer home range), probably because of both the greater number of the inhabitants (overwintering community instead of the female and her last litter in summer), and because of the shortage of available food requiring a larger feeding area for these herbivorous animals. In the peak years the impossibility of such an enlargement of activity radius, caused by population density, might contribute much to intensify competition for food and to bring on a crash situation. In spring the overwintering communities dissolve by scattering.

Furthermore, a behaviour mechanism of highest importance is involved in the nest communities of the females (Frank, 1953a). Increasingly with population condensation, the young females remain together, occupy a common territory, and bring up their litters in a single nest by means of social breeding care. Generally they remain together for the rest of their lives, and if they change their home range because of disturbance, etc., they move as a community, often with their young also. The nest community can consist of 2-4 (perhaps 5) sisters, and sometimes of their mother too. The decisive influence of this behaviour upon the population dynamic is that it enables these primarily territorial animals to live in an abnormally high density. In this way not only more females can live in the same space, but also a correspondingly greater number of young can be produced and brought up. Doubtless this particular social behaviour of *M. arvalis* explains the uncommon population density and the outright explosive population increase in plague centres, i.e., those parts of the plague districts ecologically most favourable and first occupied by the voles.

In contrast to the females, the mature males cannot draw so near to one another because they generally display rivalry (except as members of a family or of an overwintering community). During population increase in a given space, the number of old males remains the same, while that of the mature females rapidly increases. Progressing with population condensation, a considerable elimination of mature males occurs (Frank, 1953a, 1954a, 1954b; Stein, 1953b). This reduction is also evident from the pellets of owls (Becker, 1954), and thus not caused by selective predation (on the males), but by intraspecific competition (among the males). In spring and summer the weaned young males, without exception, leave their birthplaces, probably because of an innate drive after maturing. They must look for a new home range and come up against all other males they meet. Whether their number diminishes by killing each other or merely by driving each other away requires further observations. A large number of the wild males show injuries, especially bites in the region of the hindquarters, and lost tails, caused by intraspecific fighting; however, these injuries might have been acquired from resident females as well as from other males.

Thus we see that the intraspecific, especially social, behaviour of the animals is of great importance to all population-dynamic events. Further research is needed on this point, especially in other cyclic species, to find out whether similar or other condensation mechanisms are prevalent.

POPULATION DECLINE

What causes the population decline of *M. arvalis*? The life span of the little microtines is naturally short. Periods of crises and losses seem to be: (1) becoming acquainted with the maternal home range first, in which there is danger if strange neighbours are encountered; (2) the period of spreading after weaning, which involves heavier losses in the males than in the females; and (3) the winter season, which normally diminishes the population up to 50 per cent or more (Frank, 1954b). The animals of my marked wild populations never survived two winters, and the markedly old individuals almost all succumb to the stresses of the first winter months. Not only those individuals that have survived a winter die, but also those born in spring and summer that had reproduced suffer mortality. Their body weight gradually diminishes throughout the autumn, and their body reserves are nearly consumed by then. In contrast, the young animals born in the autumn increase in weight and lose only a little in the beginning of winter; then their weight is maintained during the winter months (mostly about 12-18g.) and mounts again quickly in early spring. While the period of spreading causes heavier losses among males, winter mortality strikes more females because they are mostly somewhat smaller and weaker (Frank, 1954b). Nevertheless, mortality effects a real selection by eliminating the less fit individuals. After the winter period, the surviving population consists nearly exclusively of autumn-born animals that had remained sexually immature until spring. The older voles, already having participated in reproduction during the last year, have vanished with only few exceptions.

Winter mortality can be so great, particularly in extremely severe winters, that the population declines to a minimum level by a gradual die-off of most individuals; but this happens only when population density is not high enough to produce a regular crash. However, the physiological mechanism of this gradual die-off seems to be similar to that of the regular crash, and to be based on the endocrine system also (see below). In this way, the stress of such a severe winter can injure the survivors of the gradual die-off (and also of a regular crash) so much that a remarkable subsequent mortality occurs among them during spring. They do not mount in weight and can hardly bring up their young, which therefore show heavy mortality. This has already been pointed out by Chitty (1952, 1955) and in every way confirmed also by my own researches in outdoor cages (Frank, 1954a) as well as by research on wild populations of *M. arvalis* and *M. agrestis* (as yet unpublished). Therefore, vole populations always have a difficult and slow start toward recovery after severe winters and after crashes. Predation plays only a very small part, because predators are not at all numerous in the plague districts, having been kept down both by the unfavourable, monotonous and coverless biotope and by human persecution (Frank, 1954b, 1955, 1956b).

In the peak years characterized by overcrowding, the regulation of microtine population density by no means shows itself as mass emigration as with the lemmings (*Lemmus lemmus* L.), for we observed movement of individuals only, more commonly in the males than in the females. As previously stated, the latter are generally inclined to settle in the neighbourhood of their birthplaces as long as they are able to find places unoccupied by other females. But space finally becomes scarce (in spite of and after reduction of the size of the home ranges) and competition among females increases. Reproduction is then gradually restricted (Frank, 1953a, 1954a). The degree of embryonal resorptions, infertility, and mortality of young all mount quickly, but population density can no longer be regulated by these; the carrying capacity of the environment has already been greatly exceeded. For this reason regulation must be performed by a more effective mechanism: the crash. Our investigations could not produce any evidence for the hypothesis that epizootic diseases or parasites cause the crash, although our material was examined by many specialists (Frank, 1953b). An explanation was only possible on the basis of Christian's (1950) important idea that the "shock disease" of the varying hare (*Lepus americanus* Erx.), discovered by Green and Larson (1938), seems to be an appearance of the general adaptation syndrome of Selye (1946).

First I must say that the crash symptoms in *M. arvalis* are the same as in *L. americanus*: lethargy, convulsions, liver degen-

eration, enlargement of the adrenals and hypoglycemia, and moreover (not mentioned by Green and Larson) marked decline in body temperature long before death, and behavioural changes such as crowding and cannibalism. The last represents an important chance for survival of the fitter individuals by making use of the carcasses of their dead companions as food reserves during the period of general deficiency or shortage of vegetable food already used up by the overcrowded population (Frank, 1953b). Not only have we found these symptoms experimentally in outdoor cages where vole populations were kept overcrowded and showed drastic crashes, but we were also able to produce crash symptoms by artificial hypoglycemia induced by insulin injections; conversely, the symptoms could be suspended, temporarily at least, by injection of grape sugar (Frank, 1953b).

We get the impression that condensation and crowding favour competition and cause a state of psychological excitement being transformed by the pituitary-adrenocortical system into a physical stress. This, acutely combined with the stress of food shortage, produces a "readiness" for crash, whether the real releasing of the crash is caused by an increase in the force of these stresses, or, in nature, largely by additional meteorological stresses, such as periods of cold or precipitation. On the whole, a situation with several stress-producing components ultimately produces the resulting "crash" either when all stress factors jointly reach a critical point or value, or when a new stress is superimposed on the already stressed adrenopituitary system.

In my opinion, our results confirm the basic trends of ideas presented by Christian's (*op. cit.*) important working hypothesis, but my results differ in one essential point. Christian supposes that the crash, the readiness for which is brought about by several stresses, is ultimately caused and released by the additional stress of the activation of gonads happening in the early spring. But I never found any enlargement of testes and uteri in crashing wild populations. Also in my experimentally induced crashes of outdoor-cage populations, activation of gonads was certainly not in play. I am therefore convinced that gonadotrophic demands are not involved in the crash phenomenon, in *Microtus* at least. In my conception the ultimate trigger, producing the crash of vole populations, is an additional stress of meteorological events, particularly frost periods. I believe that this conception explains better than Christian's the sudden advent of a crash within a few days. The stress of gonadotrophic demands would be extended over longer time and would operate in very different moments upon the single animal. In contrast, the meteorological stress caused by the intrusion of frost periods acts equally and suddenly upon all individuals and makes more easily understandable the suddenness of the crash.

Nevertheless, gonadotrophic activation might play an essential role, indeed, in the subsequent mortality occurring in spring among the survivors from crashes and gradual winter die-offs, which was discovered by Chitty (*op. cit.*) and also found in the vole populations investigated by the author (see above). In this case, gonadotrophic activation presents a true additional stress upon the endocrinological system, as Christian has supposed.

I must emphasize that this conception is based on investigations in vole populations only. In any event, it now seems to be certain that the adreno-pituitary system has decisive importance in intraspecific regulatory events occurring in vertebrate populations. Further research is needed to complete and deepen our knowledge of this important point, and to find out in what manner and with which different effects this psycho-physiological mechanism is operating and which environmental factors are acting upon them, in voles as well as in other rodents and vertebrates generally.

THE PERIODICITY OF CYCLES

Many workers on the periodicity of cycles (recently again Siivonen and Koskimies, 1955) attempt to connect this problem with cosmic factors before having explored all terrestrial environmental factors possibly influencing it. But nearly all such work on this subject generally seems to suffer from the fact that the phenological data, particularly the meteorological conditions, are not brought into relationship as the most important environmental factors acting upon cyclic populations. Favoured by the extremely equalized temperate climate in the Gulf Stream neighbourhood of northwestern Germany, Maercks (1954) has been able to

evaluate the interaction between the cycles of *M. arvalis* and meteorological events over a period of 39 years, based on the five-day median values of temperature, quantity and frequency of precipitation, and duration of sunshine. Therefore the cyclic events take place in a rather "pure culture" generally little influenced by extreme changes in weather conditions, which—if they occurred —could easily be analysed regarding their effects on the cyclic events. Maercks found a clear and strict microtine-cycle periodicity of three years from peak to peak, obviously caused by the reproductive and condensation potential of the species and the carrying capacity of its environment. Under optimal environmental conditions *M. arvalis* is able to replenish a plague district within three years so completely that the carrying capacity is exceeded and natural regulation by crash must occur. Every population has its own autonomous periodicity, and in other spheres (other species or other environment, or both) there will be other frequencies of the periodicity (Frank, 1954b). Dymond (1947) has already suggested that animals with a high and constant reproductive potential may be able to populate deficiently buffered[2] biotopes of optimal and constant ecological conditions at regularly occurring intervals to an unbearable density.

As to the influence of meteorological conditions, Maercks (*ibid.*) found frequent quantitative oscillations in the degree of the peak population density and plague damage, but few temporal mutations of the periodicity itself. The former are caused by changes of rainfall and duration of sunshine, for example, while the latter are all reducible to uncommon and extreme deviations in weather conditions, especially in winter. In the 39 years investigated by Maercks, the three-year periodicity has undergone three mutations, which led to the following conclusions: (1) A particularly mild winter prolongs the plague over a two-year period, and therefore the cyclic interval extends to four years, because the expected crash does not happen but comes a year later; (2) an extremely long and severe winter cuts off the population increase by causing a gradual die-off or a precocious crash and forcing a new start of population increase.

In both cases the cycle periodicity suffers a shifting of phase by one year (or more perhaps in other cases). This shifting, indeed, is a point in the cycle phenomenon that has caused considerable difficulty to cycle workers, who have almost established a periodicity of 3 1/3 years. But this was unsatisfactory because the cyclic periodicity is based (in my opinion at least) on the reproductive season's being fixed by the astronomical year. Every biological periodicity extended over several years might also present whole numbers corresponding to the whole numbers of years. This difficulty is removed by the shifting of phase caused by meteorological deviations that occur in every climate; the phase shift easily explains the fact that animal cycles never show a symmetrical periodicity over a long period of time but always show a few exceptions or deviations from the prevailing equal periodicity (three years in the case of *Microtus arvalis*).

Also the striking conformity in the periodicity of different cyclic populations and plague districts, independent of and isolated from each other, is produced by meteorological conditions prevailing equally over a large region (Frank, 1954b). For example, an uncommon and extremely severe winter will simultaneously throw back all populations influenced by it (each having its own autonomous periodicity previously), to a new (and common) starting point. Nevertheless, some populations exposed to special environmental conditions can show a different periodicity, most commonly because favourable overwintering conditions have counterbalanced unfavourable meteorological conditions.

SUMMARY

The results of recent work on microtine cycles occurring in Germany enable us to understand this phenomenon as an interaction between biotic and environmental factors only, and without aid of any hypothetical explanation by extraterrestrial "cosmic" factors. It may be supposed that the causality of other animal cycles will find a similarly "natural" explanation after being explored as intensively as the cycles of *Microtus arvalis* in Germany. Although these

[2]These are biotopes with a scarcity of natural counterpowers to the species in question, as enemies, competition by other species, limit of food and habitats, or other unfavourable ecological conditions.

are indeed "released" by human cultivation measures, which have produced optimal biotopes and thus the ecological base of cycles, the biotic causalities and laws of these cycles must be the same as those prevailing in cycles occurring in natural districts not influenced by man.

Concerning *M. arvalis* the population increase is based on: (1) a high reproductive potential based on (a) extremely early maturity and mating (in females often before being weaned), (b) high reproductive efficiency (litter weights to 53.2 per cent of the mother's weight), (c) large litter size (maximum 12-13, average in wild populations about 7 young), (d) rapid litter succession (pregnancy about 20 days, postpartum mating normal), and (e) extended season of reproduction (sometimes throughout winter); (2) a high carrying capacity of the environment under the optimal ecological conditions of the plague districts, based on food, cover, ground-water level, sunlight, overwintering places, and last but not least on the uniform structure of the landscape; and (3) a high "condensation potential" based on behaviour, particularly social mechanisms concerning (a) reducible home-range size during population increase, formation of (b) "great families" and (c) overwintering communities, (d) communal nesting of females, and (e) elimination of males. On the whole, these factors sufficiently explain the outright explosive increase and the uncommon density of microtine populations in German plague districts.

Because this rapid population increase cannot be regulated by normal mortality and dispersal, more efficient regulatory mechanisms are called into play. When the supportable density of population is approached, restriction of reproduction and accelerated individual emigration take place, but these are not enough to keep the population within the limits set by the carrying capacity of the environment. When supportable density is exceeded, crash, caused by shock disease, occurs in the following winter. Psychological stresses (such as crowding and competition) and physical stresses (such as food shortage) produce a "readiness" for crash, but the real trigger is largely the additional meteorological stress of winter. Three years are ordinarily required to reach this point, hence an autonomous and strict 3-year periodicity exists. The seldom-occurring deviations ("shifting of phase") are caused only by uncommon meteorological conditions. Unusually severe winters synchronize the periodicity of isolated populations over large districts.

On the whole, cycles take place where the high biotic potential of the species is fully realizable in the optimal biotopes of plague or other cyclic districts. It seems remarkable that this disproportion is not balanced by selection. Cycles have undoubtedly gone on from time immemorial, and the quick succession of generations of voles should have favoured such an adaption in a relatively short time.

LITERATURE CITED

BECKER, K. 1954. Beiträge zur Geschlechtsbestimmung von Mäusen (Muridae) nach Skelettresten aus Eulengewöllen. Zool. Jahrb. (Systematik), 82:463-472.

CHITTY, D. 1952. Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire, in 1936-39. Phil. Trans. Roy. Soc. London, Ser. B, 236:505-552.

———. 1955. Adverse effects of population density upon the viability of later generations. Pp. 57-67 *in*: "The numbers of man and animals," edited by J. B. Cragg and N. W. Pirie. Oliver and Boyd, Edinburgh. 152pp.

CHRISTIAN, J. J. 1950. The adreno-pituitary system and population cycles in mammals. J. Mamm., 31:247-259.

DYMOND, J. R. 1947. Fluctuations in animal populations with special reference to those of Canada. Trans. Roy. Soc. Canada, Ser. III, 16:1-34.

FRANK, F. 1952. Umfang, Ursachen und Bekämpfungsmöglichkeiten der Mäusefrassschäden in Forstkulturen. Nachrichtenbl. Deutsch. Pflanzenschutzdienst (Braunschweig), 4:183-189.

———. 1953a. Zur Entstehung übernormaler Populationsdichten im Massenwechsel der Feldmaus, *Microtus arvalis* (PALLAS). Zool. Jahrb. (Systematik), 81:610-624.

———. 1953b. Untersuchungen über den Zusammenbruch von Feldmausplagen (*Microtus arvalis* PALLAS). Zool. Jahrb. (Systematik), 82:95-136.

———. 1953c. Zur Entstehung neuer Feldmausplagegebiete durch Moorkultivierung und Melioration. Wasser und Boden (Hannover), 5:342-345.

———. 1954a. Beiträge zur Biologie der Feldmaus, *Microtus arvalis* (PALLAS). Teil I: Gehegeversuche. Zool. Jahrb. (Systematik), 82:354-404.

———. 1954b. Die Kausalität der Nagetier-Zyklen im Lichte neuer populationsdynamischer Un-

tersuchungen an deutschen Microtinen. Zeitschr. f. Morphol. u. Oekol., 43:321-356.

———. 1955. Naturschutz und Mäuseplagen. Natur und Landschaft (Lüneburg), 30:109-112.

———. 1956a. Beiträge zur Biologie der Feldmaus, *Microtus arvalis* (PALLAS). Teil II: Laboratoriumsergebnisse. Zool. Jahrb. (Systematik), 84:32-74.

———. 1956b. Grundlagen, Möglichkeiten und Methoden der Sanierung von Feldmausplagegebieten. Nachrichtenbl. Deutsch. Pflanzenschutzdienst (Braunschweig), 8:147-158.

——— AND K. ZIMMERMANN. 1956. Zur Biologie der Nordischen Wühlmaus (*Microtus oeconomus stimmingi* NEHRING). Zeitschr. f. Säugetierkunde, 21:58-83.

———. 1957. Die Verwendbarkeit morphologischer Merkmale als Alterskriterien bei der Feldmaus, *Microtus arvalis* (PALLAS). Zool. Jahrb. (Systematik), 85: in press.

GREEN, R. G. AND C. L. LARSON. 1938. A description of shock disease in the snowshoe hare. Amer. J. Hyg., 28:190-212.

MAERCKS, H. 1954. Über den Einfluss der Witterung auf den Massenwechsel der Feldmaus (*Microtus arvalis* PALLAS) in der Wesermarsch. Nachrichtenbl. Deutsch. Pflanzenschutzdienst (Braunschweig), 6:101-108.

MÜLLER, H. 1954. Zur Fortpflanzungsbiologie des Hermelins (*Mustela erminea* L.). Rev. Suisse Zool., 61:451-453.

REICHSTEIN, H. 1957. Feldmaus, *Microtus arvalis* (PALLAS 1779), mit 13 Embryonen. Säugetierkundliche Mitt., 5: in press.

SELYE, H. 1946. The general adaptation syndrome and the diseases of adaptation. J. Clin. Endocrinol., 6:117-230.

SIIVONEN, L. AND J. KOSKIMIES. 1955. Population fluctuations and the lunar cycle. Papers on Game Research (Helsinki), 14:1-22.

STEIN, G. H. W. 1953a. Über Umweltabhängigkeiten bei der Vermehrung der Feldmaus, *Microtus arvalis*. Zool. Jahrb. (Systematik), 81:527-547.

———. 1953b. Über das Zahlenverhältnis der Geschlechter bei der Feldmaus, *Microtus arvalis*. Zool. Jahrb. (Systematik), 82:137-156.

Received for publication October 9, 1956.

RESPONSES OF FORAGE TO TIMBER STAND IMPROVEMENT IN THE MISSOURI OZARKS

Thomas S. Baskett, Robert L. Dunkeson, and S. Clark Martin[1]

Cooperative Wildlife Research Unit, University of Missouri, Columbia; Missouri Conservation Commission, Columbia; and Central States Forest Experiment Station, Columbia, Missouri

The amount of deer forage produced in forest stands is influenced greatly by the type of forest management practiced in the stands. In the Missouri national forests, about 30,000 acres are being cut selectively each year; approximately 83 per cent of this acreage receives follow-up timber stand improvement consisting of killing cull trees. This type of management helps offset the progressive closure of the forest canopy resulting from effective protection against fire, and releases low-growing plants in the small openings scattered throughout the forest. Although it is apparent that the amount of deer forage often increases in these openings, quantitative data on the nature of these increases are few.

The present study was designed to provide such data for a release made by girdling cull trees in a post oak–blackjack oak stand with dense tree reproduction. This study was similar to one we reported earlier (Martin, *et al.*, 1955,) which, however, tested effects of release under seemingly more favorable conditions for forage species, i.e. a white oak site with sparse tree reproduction. This study also had some similarity to that made by Cassady (1952), who showed that the yield of bluestem grasses more than doubled three years after scrub hardwoods were controlled on an area in central Louisiana.

LOCATION

The present study was made on a 12.5-acre area in the Missouri national forests in Phelps County. Two-thirds of the area was nearly level with fine-textured top soils; the remainder was a stony south-facing slope. The scattered dominant overstory of this

[1]Martin now at Rocky Mountain Forest & Range Experiment Station, Tucson, Arizona. The writers are indebted to L. W. Hornkohl and P. D. Dalke for laying the groundwork of this study.

two-storied forest consisted of post oak (*Quercus stellata*[2]), blackjack oak (*Q. marilandica*), black oak (*Q. velutina*), and Buckley's hickory (*Carya texana*). In 1955, after several cull trees girdled in 1950 had died, the dominant overstory consisted of 15 to 20 trees per acre, of which about five were merchantable. The understory consisted of more than 4,200 three- to twelve-foot hardwood sprouts per acre. As shown by annual rings, all the sprouts dated from the last general fire in the early 1930's. Browse, forbs, and perennial grasses were sparse.

Although a few cedars (*Juniperus virginiana*) and short-leaf pines (*Pinus echinata*) had been planted in one portion of the study area during the 1930's, no recent logging or timber stand improvement had been conducted in the immediate vicinity prior to the start of this study in 1950. Recent grazing by cattle was negligible, and deer pressure was light.

PROCEDURE

In August 1950, all cull trees in each of three parallel strips, 233 feet by 700 feet, were girdled according to the Forest Service procedure that was then standard; no herbicides were used. Noncommercial species (blackjack oak and Buckley's hickory) larger than 4 inches d.b.h. were girdled, as were cull trees of merchantable species (post oak, black oak, and a few white oaks, *Q. alba*). Three similar check strips were alternated with the three girdled strips.

Frequencies of forage species were sampled around three large "hub" trees in each strip. Thirteen circular one-square-foot plots were located at two-foot intervals along three 25-foot lines radiating from each hub tree. Thus, there were 351 one-square-foot plots in the girdled strips, and an equal number in the untreated strips.

About half the plots were underneath the crowns of hub trees. In the treated strips, all hub trees were girdled; thus it was assured that most of the plots were subjected directly to overhead release.

The record for each one-square-foot plot was a list of species occurring upon it, and summaries were expressed as the average number of species per plot. Crown cover of all trees more than 10 feet tall was used as a measure of overstory influence; the presence of crown cover was recorded if one or more trees overhung a plot. Other classes of vegetation recorded were: tree reproduction, palatable browse, grasses, and forbs. Tree reproduction included trees less than 10 feet tall overhanging the centers of the plots. Palatable browse included shrubs, vines, and small trees of species palatable to deer in Missouri (Dunkeson, 1955). Browse was tallied if rooted within the plots or if it overhung the plots at heights of less than 5 feet. Grasses and forbs were included only if rooted within the plots.

All records of vegetation obtained were actually based on frequencies. However, frequencies of the important grasses, forbs, and browse species were relatively low, and under such conditions frequency is a good indicator of abundance (McGinnies, 1934).

RAINFALL

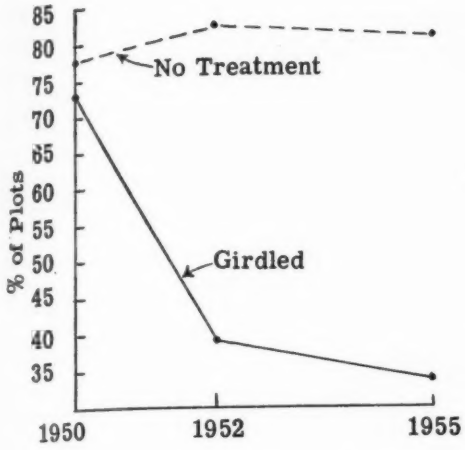
Results of this study were affected decidedly by rainfall. The growing season of 1951 (the first after girdling was performed) was abnormally wet. According to weather data taken or estimated from U.S. Weather Bureau Annual Summaries for Missouri, rainfall at Rolla, 17 miles from the study area, was 56.1 inches in 1951—14.6 inches more than the average annual amount. For the next four years, however, rainfall was less than normal; in fact there were two of very severe drouth. Approximate departures from normal at Rolla were as follows: 1951, +14.6 inches; 1952, –12.7 inches; 1953, –15.9 inches; 1954, –5.3 inches; and 1955, –3.8 inches. A few large trees died, probably as a result of drouth, and forbs declined precipitously over the five years in both girdled and untreated strips. Other types of vegetation were not so noticeably affected, but even for them, the value of the following data lies principally in comparisons of vegetation in girdled and untreated plots, rather than in increases within the girdled plots.

RESULTS

Crown cover showed the expected decline following girdling (Fig. 1). In the untreated strips, crown cover changed but little, with slight gains from growth being partially offset by drouth kill.

Tree reproduction increased moderately in the girdled strips over the five-year pe-

[2]Nomenclature as given by Fernald (1950).



Year	Girdled	No Treatment
1950	73.2%	77.5%
1952	39.9	82.3
1955	34.7	80.9

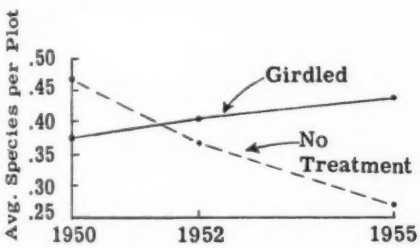
Fig. 1. Per cent of plots under tree crowns

riod, but since this class of vegetation declined in the untreated strips, the frequency at the end of the study was much greater in girdled than in untreated strips (Fig. 2A). In all strips, some of the small trees classed as reproduction in 1950 later attained 10-foot heights and were thus removed from this class. In the girdled strips, rapid growth of small reproduction more than compensated for this loss, while in the untreated strips, the small reproduction grew very little. There was apparently little drouth kill of reproduction.

Palatable browse, which was sparse throughout, increased in the girdled strips and decreased in the untreated ones (Fig. 2B). Most of the increase was blueberries (*Vaccinium* spp.). Other browse species included short-leaf pine, sassafras (*Sassafras albidum*), and New Jersey tea (*Ceanothus americanus*).

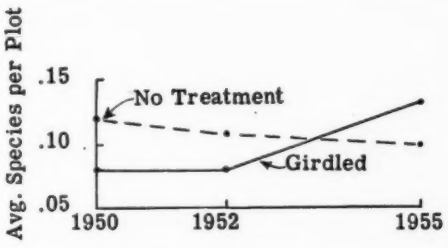
In the girdled strips, the abundance of forbs remained constant through the growing season of 1952, with release presumably offsetting effects of drouth. Three more dry years were too much, and forbs had declined sharply by October 1955 (Fig. 3A). However, the decline was greater in the untreated strips; thus the average number of species of forbs per plot was seven per cent higher in girdled than in untreated strips in 1950, but 35 per cent higher in 1955. The most abundant forbs included pussy's toes (*Antennaria plantaginifolia*), goldenrods (*Solidago* spp.), asters (*Aster* spp.), vine lespedezas (*Lespedeza procumbens* and *L. repens*), and tick clovers. (*Desmodium* spp.). Several of these species are seasonally important deer foods in Missouri (Dunkeson, 1955).

Initial abundance of grasses and sedges was lower than that of forbs, but grasses were seemingly less affected by drouth



Year	Girdled	No Treatment
1950	.38	.47
1952	.40	.37
1955	.43	.27

A. TREE REPRODUCTION



Year	Girdled	No Treatment
1950	.08	.12
1952	.08	.11
1955	.13	.10

B. PALATABLE BROWSE

FIG. 2. Average number of species of tree reproduction and palatable browse per plot on girdled and untreated strips

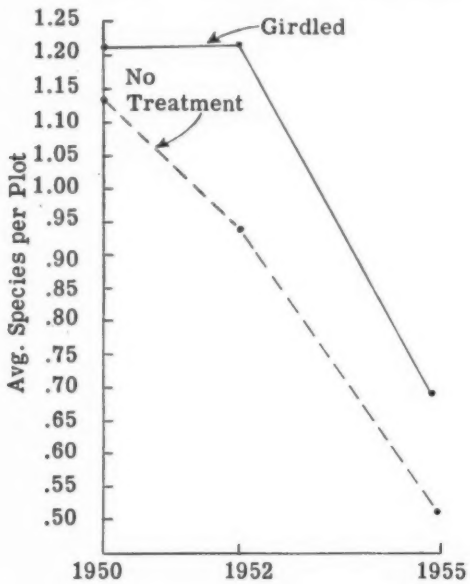
(Fig. 3B). During the study period, grasses increased in abundance in the girdled strips, but decreased in the untreated ones. In 1950, the average number of species per plot was only nine per cent greater in the girdled strips, but by 1955, the figure was 72 per cent. The increase in the girdled strips was almost entirely poverty oat-grass (*Danthonia spicata*) and little bluestem (*Andropogon scoparius*). Sedges (*Carex* spp.) were an important component of this type of vegetation, but changed little in frequency throughout the study.

TABLE 1. — RELATIVE ABUNDANCE OF FORAGE IN GIRDLED VS. UNTREATED PLOTS IN TWO OZARK FOREST TYPES

Class of Forage	Post Oak–Blackjack with Dense Reproduction (This Study)	White Oak with Sparse Reproduction (Martin, *et al.* 1955)
	Per cent	Per cent
Browse	+30	+39
Grasses and sedges	+72	+89
Forbs	+35	+24

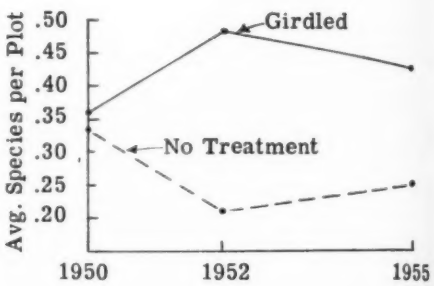
DISCUSSION

The responses of forage plants to overstory release in this study (as determined by comparing frequencies in treated and untreated plots) were similar to results obtained in an earlier study of a white oak type (Table 1). However, as a result of the combined effects of drouth and differences in



Year	Girdled	No Treatment
1950	1.21	1.13
1952	1.22	.94
1955	.69	.51

A. FORBS



Year	Girdled	No Treatment
1950	.36	.33
1952	.48	.21
1955	.43	.25

B. GRASSES

FIG. 3. Average number of species of forbs and grasses per plot on girdled and untreated strips

FIG. 4. (*right, top*) Successful forage release five years after girdling. Girdled hub tree is in center background.

FIG. 5. (*right, bottom*) Tree reproduction was released by girdling this hub tree, but little forage was produced.

forest stands, the release in the post oak–blackjack type in this study was not as successful as that in the white oak type. At the end of this study, frequencies of forage were only one-half to two-thirds as great as those of the earlier study. Further, it was readily apparent that the volume of forage produced in the white oak type was much greater, even though volumes were not actually measured.

Nevertheless, our frequency data show that measurable, beneficial effects on many species of forage used by deer can result from timber stand improvement in Missouri, even in post oak–blackjack oak types with dense advanced tree reproduction. This is a desirable by-product of a standard silvicultural practice; where a 10-year cutting cycle is practiced, repeated replenishment of forage can be expected.

Where forage release for game might be a primary objective, as on some state-owned lands, the game manager may find more effective methods. For example, a method that suppresses rather than encourages tree reproduction is needed, and several herbicides are promising in this connection.

In this study, the sample areas radiating from only four girdled trees contributed nearly 75 per cent of the total forage tallied under all nine girdled trees (Figs. 4 and 5). This fact suggests that for forage release, some attention might well be given to selection of cull trees with some forage and little or no reproduction already present under them.

SUMMARY

Effects of release of browse, grasses, and forbs in a post oak–blackjack oak type having dense tree reproduction were studied quantitatively. Release was accomplished by girdling cull trees on a study area in the Missouri national forests, according to regular Forest Service procedure.

Although a severe drouth affected results, tree reproduction and all classes of forage were much more abundant on released than on unreleased areas after five years. At the end of the study period, frequency of browse was 30 per cent greater in released than in unreleased strips; comparable figures for other classes of forage were: grasses and sedges, 72 per cent; and forbs, 35 per cent.

Even in this post oak–blackjack oak stand with dense tree reproduction, standard silvicultural procedure favored production of forage. However, where forage release is a primary objective, cull trees with desirable forage plants and little tree reproduction under them might profitably be selected for girdling. If tree reproduction is abundant, selective application of herbicides may be desirable.

LITERATURE CITED

CASSADY, J. T. 1952. Grass production doubled by the control of scrub oak. J. For., 50:462-463.

DUNKESON, R. L. 1955. Deer range appraisal for the Missouri Ozarks. J. Wildl. Mgmt., 19:358-364.

FERNALD, M. L. 1950. Gray's manual of botany (8th edition). Amer. Book Co., N.Y. 1632pp.

MARTIN, S. C., R. L. DUNKESON, AND T. S. BASKETT. 1955. Timber harvests help offset forage decline in Missouri's managed forests. J. For., 53:513-516.

MCGINNIES, W. G. 1934. The relation between frequency index and abundance as applied to plant populations in a semiarid region. Ecology, 15:263-282.

Received for publication August 4, 1956

REPRODUCTION OF CARP, LARGEMOUTH BASS, BLUEGILLS, AND BLACK CRAPPIES IN SMALL REARING PONDS[1]

Donald Mraz and Edwin L. Cooper[2]

Wisconsin Conservation Department, Madison, Wisconsin

The carp (*Cyprinus carpio*) was successfully introduced into lakes and streams of Wisconsin and other midwestern states about the year 1883. The popularity of this introduction, however, was short-lived, and control measures were quickly sought to prevent the carp from dominating the fish populations in many lakes and streams. Since that time, the detrimental effects of large carp populations on aquatic vegetation have been well documented (Cahn, 1929; Black, 1946; Moyle, 1949; Rose and Moen, 1953; Cahoon, 1953; and Threinen and Helm, 1954), but competition between carp and other fishes is not so clearly understood.

Pairs of adult carp, when placed in small ponds without other species of fish present, produced abundant crops of young in each of the 13 trials conducted over a three-year period (Mraz and Cooper, 1957). The studies reported on here were designed to determine the success of natural reproduction and early survival of carp, largemouth bass (*Micropterus salmoides*), bluegills (*Lepomis macrochirus*), and black crappies (*Pomoxis nigro-maculatus*) in small ponds with mixed populations of adult fish at known densities. Four ponds at Delafield, Wisconsin, formerly used to rear largemouth bass and bluegills, were made available for these experiments. These ponds are referred to as numbers III, IV, V, and VI. Ponds I and II were unsuitable for use during this period.

Largemouth bass and bluegills were selected as game fish to be studied because of their popularity and widespread distribution in areas where carp occur abundantly. Black crappies were also selected for study because they have remained abundant in many lakes where carp also have been abundant despite continued removal by state fishing crews. In three smaller lakes where fish populations were destroyed by rotenone, carp, black crappies, and bluegills were the dominant fishes found. Despite the lesser popularity of the crappies in this area, it was considered desirable to include them in these experiments.

Stocking the Ponds

The adult fishes were obtained from natural populations in lakes in southern Wisconsin. The carp came from rough fish operations. The game fishes were captured in fyke nets set specifically for these tests. Four combinations of largemouth bass, bluegills, black crappies, and carp were tested in each of the two years (Table 1).

The initial stocking rate of adult fishes used in 1953 (Table 1) was suggested by the species composition and population density found in several small lakes in southern Wisconsin treated with rotenone (Threinen and Helm, 1952; Mraz and Threinen, 1953 and 1954). Because a high mortality of adult game fish resulted with this stocking rate, the rate was reduced by one-half during 1954. As will be shown later, a high mortality among the introduced game fishes was again experienced in 1954.

To cut down mortality due to handling, a prophylactic treatment of malachite green was used prior to planting in the ponds. Urethane was also used to anesthetize the fish prior to measuring and weighing them. The carp and largemouth bass were selected to assure maturity, similar sizes, and balanced sex ratios in the individual ponds because of the small numbers of fish involved. The large numbers of adult bluegills and black crappies stocked made such selection unnecessary (Table 1).

The stocking quotas listed in Table 1 are close approximations of the actual densities of brood fish that were present at the time spawning began. The impossibility of selecting fish of the proper size to conform exactly to the stocking quotas resulted in

[1] A contribution from Federal Aid in Fish Restoration Project F-3-R, Wisconsin.

[2] The latter is now with the Department of Zoology and Entomology, Pennsylvania State University, University Park, Pennsylvania.

TABLE 1. — STOCKING RATE, SURVIVAL AND GROWTH OF ADULT FISHES IN PONDS FOR 1953 AND 1954

Pond Number (and Size in Acres)	Species of Fish	Adult Fish Stocked				Adult Fish Recovered		
		Stocking Quota (Pounds per Acre)	Number of Individuals	Average Total Length in Inches	Average Weight in Pounds	Percentage Survival	Average Total Length in Inches	Average Weight in Pounds
				1953				
III	Largemouth bass	40	46	14.4	1.6	67.4	14.7	1.6
	Bluegills	160	1,028	7.0	0.28	47.1	7.5	0.30
(1.81)	Carp	200	81	20.3	4.5	97.5	21.4	5.2
IV	Largemouth bass	40	22	15.4	1.9	81.8	15.4	1.9
	Bluegills	60	221	7.1	0.29	45.1	8.2	0.43
(1.07)	Black crappies	100	134	10.8	0.80	82.8	10.9	0.68
V	Largemouth bass	40	14	15.3	2.1	57.1	15.9	2.3
(0.78)	Black crappies	160	191	10.1	0.65	10.5	9.8	0.53
VI	Largemouth bass	40[1]	234	14.7	1.9	46.6	14.8	1.7
	Bluegills	60	1,592	7.4	0.33	34.9	8.0	0.25
(8.80)	Black crappies	100	1,527	10.1	0.60	59.2	10.2	0.57
	Carp	200	410	20.4	4.3	97.1	22.0	5.6
				1954				
III	Largemouth bass	20	24	13.7	1.5	20.8	14.4	1.9
	Bluegills	80	448	7.5	0.32	36.6	7.8	0.32
(1.81)	Carp	200	63	22.1	5.8	95.2	22.2	5.3
IV	Largemouth bass	20	14	14.2	1.6	64.3	14.5	1.7
	Bluegills	30	76	8.2	0.44	35.5	8.6	0.52
(1.07)	Black crappies	50	109	9.6	0.49	42.2	10.2	0.62
V	Largemouth bass	20	12	13.4	1.3	91.7	13.7	1.4
(0.78)	Black crappies	80[2]	128	10.1	0.58	27.3	10.2	0.58
VI	Largemouth bass	20	111	14.2	1.6	40.5	14.5	1.6
	Bluegills	30	707	7.8	0.42	17.7	8.5	0.49
(8.80)	Black crappies	50	809	10.0	0.55	19.8	10.4	0.63
	Carp	200	348	21.2	5.1	94.3	21.1	4.5

[1] Actually stocked at 50.5 lbs. per acre to compensate for mortality immediately evident after stocking.
[2] Actually stocked at 95.2 lbs. per acre to compensate for mortality immediately evident after stocking.

minor discrepancies. However, rather large errors in the rate of stocking occurred when heavy mortality affected a species soon after the pond was initially stocked, such as for the black crappies in Pond V in 1954. In two cases like this, additional fish were added to the pond.

In both years the ponds were stocked in April and early May. This was well in advance of the date when spawning activity began either in the experimental ponds or in lakes in the immediate vicinity.

DESCRIPTION OF THE PONDS

The ponds used in these experiments were 0.78, 1.07, 1.81, and 8.80 acres in size. The maximum depth ranged from 3 to 6 feet. A gravel filter located at the head of the water supply pipe in Nagawicka Lake ade-

quately prevented the invasion of the ponds by fish present in the lake.

Because of the shallowness of the ponds, water temperatures followed air temperatures quite closely. In both years, a water temperature of 60° F. was reached during the week of May 15, with a diurnal variation during this period of as much as 15° F. In July and August water temperatures in the 80's were common, with a peak of 87° F. being recorded.

Decomposed plant materials formed the bulk of bottom materials in the ponds. The only sand and gravel present was that used on the pond dikes or around inlet and outlet structures. The ponds were originally constructed about 50 years ago, and the accumulation of bottom deposits was partially removed about 15 years ago.

All of the ponds had abundant growths of aquatic vegetation, with very little of the pond bottom exposed. The most abundant plants were several species of pondweeds (*Potamogeton*), coontail (*Ceratophyllum*), waterweed (*Elodea*), cattail (*Typha*), watermilfoil (*Myriophyllum*), water buttercup (*Ranunculus*), bulrush (*Scirpus*), and musk grass (*Chara*).

Sporadic control of aquatic vegetation by mechanical and chemical means was effective in reducing waterweed, prickly-leaf pondweed, and cattails in Pond VI, although other plants remained abundant. However, no control was attempted in the other three ponds dominated by musk grass. Blooms of filamentous algae occurred only occasionally and never became dominant. The blue-green algae never became abundant enough to cause a noticeable turbidity, and the ponds remained very clear except for Pond VI in which the bottom mud was kept in suspension through the activity of the carp.

TURBIDITY

Perhaps the most noticeable change in the aquatic environment accompanying a large carp population is the increased turbidity of the water. This is especially true when the lake-bottom soil is easily kept in suspension by the physical activity of the carp. Although the effects of turbidity on different fishes, in our opinion, have been inadequately described, turbidities in excess of 100 p.p.m. have been shown to be detrimental to the population of certain warm-water species, among which was the largemouth bass (Schneberger and Jewell, 1928). Indirect effects of increased turbidity on the production of fish foods may depress fish production as much as direct effects on inhibiting successful reproduction (Buck, 1956).

Adult carp were planted in Ponds III and VI at the rate of 200 pounds per surface acre (Table 1). In Pond III where the bottom was composed predominantly of fibrous plant materials, the water remained clear throughout both summer periods. In Pond VI, the bottom was a mixture of loam and plant fibers. In both years, Pond VI rapidly became turbid and remained so until the pond was drained in the fall. Turbidity measurements were made with a Secchi disc, with a few parallel readings made with a Jackson turbidimeter. A maximum turbidity reading at the surface of Pond VI of 16 inches with the Secchi disc corresponded to a reading of 44 p.p.m. on the Jackson turbidimeter. At this station, the turbidity increased with depth to a reading of 52 p.p.m. at 4 feet. The average turbidity in Pond VI throughout the two seasons measured 25 to 30 inches by the Secchi disc and thus was far below the value credited by Schneberger and Jewell (1928) and Buck (1956) as being directly detrimental to fish production.

SURVIVAL AND GROWTH OF ADULT FISH

Adult fish were stocked in the ponds during April or May and the ponds were drained during September. For this five-month period, the survival of carp far exceeded the survival of the other fishes (Table 1). The average percentage survival rates for the four species for both years combined were as follows: carp, 95.9; largemouth bass, 49.5; bluegills, 35.8; and black crappies, 44.0. Despite our care during the netting and transportation procedures, some of the loss of the game fish appeared to be caused by the events associated with stocking the ponds: a noticeable mortality was observed only during the first 10 days after stocking.

The mortality rates of the adult game fishes did not appear to be closely associated with either the density of game fishes stocked in the pond or the competition with carp. Game fishes were stocked in 1953 at a combined rate of 200 pounds per acre in

each pond, with or without an additional 200 pounds of carp per acre (Table 1). When high mortalities of game fishes occurred at this stocking rate, overcrowding was suspected. However, a reduction of the stocking rate of game fishes in 1954 to 100 pounds per acre was accompanied by a greater mortality than was experienced in 1953. Game-fish mortality in ponds without carp was not noticeably lower than in ponds with the added carp competition, with the possible exception of the largemouth bass (Table 1).

The growth of the adult fish stocked in the ponds was negligible in all cases except for the carp. In Ponds III and VI in 1953 only, carp gained about an inch in length and about one pound in weight during the five-month summer period. In view of (a) the rather large average size of the adult fishes stocked, (b) the moderate to heavy stocking rates employed, and (c) the excessive abundance of aquatic vegetation, the slight growth of the adult fishes was not unexpected.

SPAWNING OBSERVATIONS

Largemouth bass began spawning in the ponds when water temperatures reached 60° F. In both years this occurred about May 15. Eggs were observed in the nests within a few days, and the fry hatched during the first week in June.

The male bass as a rule selected a sand or gravel bottom upon which to build a nest. However, in Pond VI with carp present, three bass nests originally constructed along a gravel shore were deserted before eggs were laid, and the bass renested within a very heavy bed of coontail and water buttercup. Based on observations of the apparent compatibility of the carp and bass during the spawning period, it is believed that the bass deserted the original nests because of the difference in turbidity, even though the maximum turbidity on the gravel bottom did not exceed 10 p.p.m. Inside the dense vegetation, the nests constructed on a bottom of mud and plant fibers produced successful hatches of bass fry.

Bluegills began nesting during the last week in May when water temperatures were in the low 70's. The males selected nest sites close to shore, using the sand and gravel bottom except for Pond VI where they chose the protected bed of vegetation in which to spawn. Some bluegill nests were still being guarded as late as July 21, several weeks after all largemouth bass nesting had ceased.

Spawning of carp was observed in the ponds on several occasions. Most of this activity occurred during the last week in May and the first week in June when water temperatures ranged from 65° to 75° F. Groups of males would congregate about one female, and the adhesive eggs were broadcast over submerged vegetation.

Some interesting observations of the egg deposition of carp in bare concrete holding tanks within the hatchery building were also made. Several large ripe females exceeding 20 pounds in weight were being temporarily held in the building for public display. Within a few days after being seined from the Nemahbin Lakes on May 26, 1954, it was noticed that they were spawning in the tank, despite the fact that there were no males present. It appeared as if they were depositing the eggs by bumping against the side of the concrete tank while swimming alongside. Soon the entire tank more than 20 feet long had a layer of eggs sticking to the bottom, and an ice scraper was necessary to peel off the eggs for disposal.

PRODUCTION OF YOUNG

Due to the difficulties inherent in estimating the number of fish present in ponds at any one time, no attempt was made to determine the total number of young fish produced until the ponds were drained in the fall. Excessive weed growth in most of the ponds and the turbidity of Pond VI prevented the visual observations of young fish such as were employed by Bennett (1954) in estimating largemouth bass fry. The data on production therefore represent the net result of natural reproduction, growth, and mortality for approximately three months after hatching. There is the possibility that a successful hatch of a particular species may have suffered a large loss through predation or competition and thus appear in the fall as poor production. The following data should be reviewed with this reservation in mind.

Production of the young of carp, largemouth bass, and bluegills was extremely erratic, with little consistency in individual

ponds from one year to the next (Table 2 and Fig. 1). It should be pointed out, however, that each of the species used demonstrated a high potential production in these ponds with the possible exception of the black crappies. Production of largemouth bass failed completely in two trials but was as high as 12,305 fish per acre in one instance and more than 8,000 per acre in two other trials. Bluegills spawned successfully in all ponds, averaging nearly 4,000 fish per acre in six trials and ranging from 494 to 13,560 young fish per acre. Production of black crappies in these small ponds was uniformly low, never exceeding 503 per acre and failing entirely in two trials out of six.

The reproduction of young carp in these experiments was surprisingly low when compared with the results obtained in the Lake Mills, Wisconsin, ponds (Mraz and Cooper, 1957). At Lake Mills when carp alone were placed in ponds, the minimum production of young in any one of 13 trials during a similar summer growing period was in excess of 98 pounds per acre. In the present four trials using centrarchids present with carp, the production of young carp was 2.5, 2.7, 3.2, and 124.0 pounds per acre, respectively.

There was little apparent correlation between the number of adult fishes stocked in the ponds and the strength of the resulting year class. For example, four ponds stocked with mature largemouth bass at the rate of 40 pounds per acre produced 0, 1,017, 5,650, and 8,776 young per acre, respectively.

TABLE 2. — PRODUCTION OF YOUNG LARGEMOUTH BASS, BLUEGILLS, BLACK CRAPPIES, AND CARP

Pond Number (and Size in Acres)	Species of Fish	Pounds of Adult Fish Stocked per Acre	Young Fish Produced		
			Number per Acre	Pounds per Acre	Average Total Length in Inches
		1953			
III	Largemouth bass	40	5,650	29.3	2.3
	Bluegills	160	1,093	5.0	2.2
(1.81)	Carp	200	7	2.5	8.9
IV	Largemouth bass	40	8,776	68.6	2.7
	Bluegills	60	785	7.5	2.7
(1.07)	Black crappies	100	130	1.9	3.1
V	Largemouth bass	40	0	—	—
(0.78)	Black crappies	160	0	—	—
VI	Largemouth bass	40	1,017	7.9	2.7
	Bluegills	60	499	2.3	2.1
(8.80)	Black crappies	100	503	4.2	2.7
	Carp	200	8	2.7	6.8
		1954			
III	Largemouth bass	20	0	—	—
	Bluegills	80	7,495	11.6	1.4
(1.81)	Carp	200	6,340	124.0	3.3
IV	Largemouth bass	20	8,608	62.4	2.6
	Bluegills	30	494	3.3	2.0
(1.07)	Black crappies	50	122	2.1	3.2
V	Largemouth bass	20	12,305	34.2	1.9
(0.78)	Black crappies	80	0	—	—
VI	Largemouth bass	20	0	—	—
	Bluegills	30	13,560	15.0	1.1
(8.80)	Black crappies	50	307	1.3	1.9
	Carp	200	97	3.2	3.8

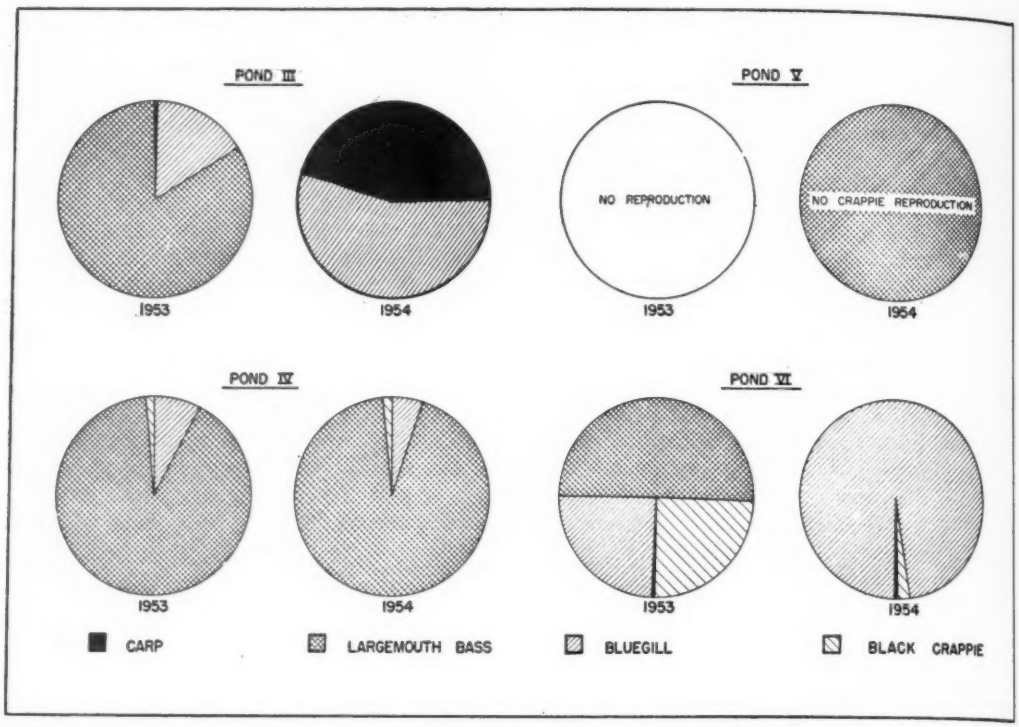


FIG. 1. Species composition of young of the year in ponds at Delafield resulting from natural reproduction. Pond III stocked with largemouth bass, bluegills, and carp; total standing crop was 6,750 fish per acre in 1953, and 13,835 fish per acre in 1954. Pond IV stocked with largemouth bass, bluegills, and black crappies; total standing crop was 9,691 fish per acre in 1953, and 9,224 fish per acre in 1954. Pond V was stocked with largemouth bass and black crappies; there were no young produced in 1953, and 12,305 fish per acre in 1954. Pond VI was stocked with largemouth bass, bluegills, black crappies, and carp; total standing crop was 2,027 fish per acre in 1953, and 13,964 fish per acre in 1954.

The same four ponds stocked the following year at 20 pounds of brood fish per acre produced 0, 0, 8,608, and 12,305 young fish per acre, respectively. Equally discrepant comparisons between brood-stock density and production of young fish were noted for both the bluegills and black crappies. These observations are also in agreement with the results of carp reproduction at the Lake Mills ponds (Mraz and Cooper, 1957), where the production of young fish appeared to have little relationship with the number of available brood fish.

DISCUSSION

An analysis of the production of young in the various pond combinations used suggests that high populations of carp may depress the production of largemouth bass. However, this is not true in all cases, for two ponds containing carp with bass yielded 1,017 and 5,650 young bass per acre. Compared with stocking rates of fingerling bass commonly employed in fish-management work, this rate of production would appear to be entirely adequate to maintain bass populations if other conditions were suitable. The authorized stocking rate in Wisconsin for lakes under 500 acres was five fingerling per acre (Schneberger, 1952). These production rates also compare favorably with the natural production of largemouth bass fry in Ridge Lake (Illinois), which maintained adequate bass populations without the need for maintenance stocking (Bennett, 1954). The reasons for complete failures of bass production are not known at this time, but failures occurred in ponds with and without carp present.

Bluegill reproduction was more consistent than that of any of the other fishes studied,

although high production in numbers did not accompany high bass production. Early spawning and rapid development of bass fry could have reduced bluegill survival through predation in these ponds, although Bennett (1954) reported high survival of bluegill fry in the face of a dense population of small largemouth bass in Ridge Lake (Illinois) in 1945 and 1946. It is obvious from these experiments and the published results of the many authors cited above that the factors affecting natural reproduction of pond fishes are many, and their relationships are complex. Pond fish culture, or the management of small lakes involving several species of game and pan fishes, thus will always be difficult and the results uncertain. But it is also apparent that natural reproduction most often results in a surplus of one species or another. Proper management usually will consist of control of this natural surplus to enable more fish of the more favored species to grow to desirable sizes.

ACKNOWLEDGMENTS

Grateful appreciation is expressed to Elmer F. Herman and C. W. Threinen for their help in planning and conducting these experiments. Credit is also due Eric Zipp and Spencer Chapman for their assistance in draining the ponds and processing the fish.

SUMMARY

The present study was designed to determine the success of natural reproduction and early survival of carp, largemouth bass, bluegills, and black crappies in small ponds with mixed populations of mature fish at known densities in southern Wisconsin.

Adult fishes were stocked in ponds in April or May, and the ponds were drained in September or October. During this period, the percentage survival of adult carp far exceeded that of the other species, as follows: carp, 95.9; largemouth bass, 49.5; bluegills, 35.8; and black crappies, 44.0.

There was little apparent correlation between the number of brood fish stocked in the ponds and the strength of the resulting year class. There was also little consistency in the success of natural reproduction of a particular species from one year to the next when the same combination of species was used to stock the ponds. The range in standing crop of the young of each species during the three-year period, expressed as the number of fish per acre, was very great: carp, 7 to 6,340; largemouth bass, 0 to 12,305; bluegills, 494 to 13,560; and black crappies, 0 to 503.

LITERATURE CITED

BENNETT, GEORGE W. 1954. Largemouth bass in Ridge Lake, Coles County, Illinois. Bull. Ill. Nat. Hist. Surv., 26(2):215-276.

BLACK, JOHN D. 1946. Nature's own weed killer —the German carp. Wis. Cons. Bull., 11(4): 3-7.

BUCK, D. HOMER. 1956. Effects of turbidity on fish and fishing. Trans. N. Amer. Wildl. Conf., 21:249-261.

CAHN, ALVIN R. 1929. The effect of carp on a small lake: the carp as a dominant. Ecology, 10(3):271-274.

CAHOON, WILLIE G. 1953. Commercial carp removal at Lake Mattamuskeet, North Carolina. J. Wildl. Mgmt., 17(3):312-317.

MOYLE, JOHN B. 1949. Fish population concepts and management of Minnesota lakes for sport fishing. Trans. N. Amer. Wildl. Conf., 14: 283-294.

MRAZ, DONALD F. AND EDWIN L. COOPER. 1957. Natural reproduction and survival of carp in small ponds. J. Wildl. Mgmt., 21(1):66-69.

——— AND C. W. THREINEN. 1953. Fish population and standing crop of Cambria Pond, a rough fish problem. Wis. Cons. Dept., Invest. Rept. No. 673 (mimeo.). 8pp.

——— AND ———. 1954. Fish population and standing crop of Potter's Lake. Wis. Cons. Dept., Invest. Rept. No. 128 (mimeo.). 23pp.

ROSE, EARL T. AND TOM MOEN. 1953. The increase in game fish populations in East Okoboji Lake, Iowa, following intensive removal of rough fish. Trans. Amer. Fish. Soc., 82(1952): 104-114.

[SCHNEBERGER, EDWARD]. 1952. Standard procedure for stocking and management of warmwater species. Wis. Cons. Dept. (mimeo.). 5pp.

——— AND MINNA E. JEWELL. 1928. Factors affecting pond fish production. Kansas Forestry, Fish and Game Comm., Bull. No. 9, 14pp.

THREINEN, C. W. AND W. T. HELM. 1952. Composition of the fish population and carrying capacity of Spauldings Pond, Rock County, as determined by rotenone treatment. Wis. Cons. Dept., Invest. Rept. No. 656 (mimeo.). 19pp.

——— AND ———. 1954. Experiments and observations designed to show carp destruction of aquatic vegetation. J. Wildl. Mgmt., 18(2): 247-250.

Received for publication October 8, 1956.

NOTES ON TOOTH DEVELOPMENT AND WEAR FOR ROCKY MOUNTAIN MULE DEER[1]

W. Leslie Robinette, Dale A. Jones, Glenn Rogers, and Jay S. Gashwiler

U.S. Fish and Wildlife Service, Salt Lake City, Utah; Utah State Fish and Game Department, Salt Lake City, Utah; Colorado Department of Game and Fish, Grand Junction, Colorado; and U.S. Fish and Wildlife Service, Corvallis, Oregon (respectively)

Many researchers have recognized the management values derivable from age-structure data for big-game herds. These same workers are in general agreement that time of dental replacement and subsequent rate of tooth wear, despite weaknesses, are the most reliable means of aging members of the deer family. Severinghaus (1949), Hayne and Eberhardt (1952), Stevens (1953), Gill (1953), Banfield (1955), and others have either pointed out the relationship of age structure among big-game animals to herd survival and mortality rates or have shown how age data may be used as a census tool. Hayne and Eberhardt (*ibid.*) have stressed that if hunter-killed deer are to reflect the herd's age structure, at least some of the age classes must be equally vulnerable to hunters. Studies by Anderson (1953) indicated that age classes in a herd of Danish roe deer (*Capreolus capreolus*) were equally vulnerable to being shot when hunter selectivity was not a factor. Severinghaus (1954) concluded that wariness did not distort age composition of the kill from that of the wild population among whitetails (*Odocoileus virginianus*) in New York, providing the hunting season was of more than two days' duration.

Age-composition studies of mule deer herds have been seriously hampered by lack of adequate dentition studies such as Severinghaus' (1949) for white-tailed deer. Dentition studies of the *Odocoileus hemionus* group have been few, and for lack of known-age specimens, have usually treated only tooth replacement (McLean, 1936; Moreland, 1952; Jones, 1953; Hunter, 1947; Cowan, 1936; Leopold, *et al.*, 1951; Robinette and Jensen, 1950; and others). Aging criteria are presented for Rocky Mountain mule deer (*O. h. hemionus*) in Utah and Colorado in this paper and, despite obvious deficiencies in the older age classes, represent some progress in the study of mule deer aging.

We wish to acknowledge the assistance rendered by the several individuals who helped ear-tag the deer that later provided known-age specimens used in this study and by Norman V. Hancock and Vergil Draney of the Utah State Fish and Game Department for collecting jaws from fawns and yearlings killed on control work during the spring and summer months. Our appreciation is also extended to LaVar Ware of the Utah State Fish and Game Department for the photographs used in this paper, to H. E. Petersen of the Chemical Laboratory of the U.S. Bureau of Mines, Salt Lake City, Utah, for fluorine analyses of deer teeth, and to biologist Fred Zwickel of the State of Washington Department of Game, and graduate student Frank B. Golley of Washington State College for providing photographs of two known-age, old deer.

Material

Most of the known-age deer providing jaws used in this dentition study were tagged as young fawns on the open range within a few hours or days following birth. However, some were trapped and ear-tagged during winter as 5- to 10-month-old fawns.

The single deer obtained in the 9-year-4-month class (Table 1) was tagged and released by Everett Doman from the Fillmore Deer Pasture in central Utah on August 28, 1940, and killed by a hunter in October 1947. Doman believed the doe to be a 2-year-old at the time of tagging because of the appearance of her incisors, lack of young, and her size which was slightly less than that of a fully matured doe. Although there is a slight possibility she could have been older, presence of all permanent incisiform teeth precluded the possibility that she was younger.

Two of the deer (age—4 yrs. 9 mos. and

[1]A contribution from the Utah cooperative big-game, livestock, and range relationship research project and the Colorado Department of Game and Fish

TABLE 1.—AGE AT TIME OF CAPTURE AND DEATH OF KNOWN-AGE MULE DEER USED IN THIS STUDY

Age at Death	Number of Specimens			
	Age When Tagged			
	1-20 Days	5-10 Mos.	Older	Total
4 days	1	—	—	1
1 week	1	—	—	1
2 weeks	1	—	—	1
4 mos.	3	—	—	3
6.5 mos.	1	—	—	1
1 yr. 4 mos.	41	3	—	44
1 yr. 7 mos.	1	—	—	1
1 yr. 10 mos.	1	—	—	1
2 yrs. 4 mos.	16	1	—	17
2 yrs. 6 mos.	—	1	—	1
2 yrs. 8 mos.	1	—	—	1
2 yrs. 9 mos.	—	1	—	1
3 yrs. 2 mos.	1	—	—	1
3 yrs. 4 mos.	5	—	—	5
4 yrs. 4 mos.	3	1	—	4
4 yrs. 9 mos.	1	—	—	1
4 yrs. 10 mos.	—	1	—	1
5 yrs. 4 mos.	2	1	—	3
8 yrs. 3 mos.	1	—	—	1
9 yrs. 4 mos.	—	—	1	1
10 yrs. 6 mos.	1	—	—	1
Totals	81	9	1	91

10 yrs. 6 mos.) had been held captive from the time they were young fawns until their death. The food they obtained differed considerably from natural forage and apparently caused atypical wear. As a consequence, their jaws have not been used, except to point out variations in dental wear that might result from different diets (discussed in greater detail under "Factors Influencing Tooth Wear and Eruption"). Three other deer (6.5 months; 1 yr. 7 mos.; and 3 yrs. 2 mos. old) were semicaptives, but most of their food consisted of native vegetation.

In Table 2 are listed basic data on tooth development and replacement for deer listed in Column 2, Table 1 (deer 1-20 days of age when tagged). Live specimens were not available in this study to provide periodic observations of tooth development and replacement. Our specimens provided a single observation per animal, since we used only the mandibles that had been removed from the deer soon after death. Most of the known-age deer were killed by hunters during October, hence our observations of tooth development and replacement throughout the year from known-age animals are necessarily incomplete. To fill in this gap, we have collected hundreds of mandibles from untagged fawns, yearlings, and 2-year-olds (since study of known-age jaws showed that these classes were readily distinguishable at least until 2-year-olds were 28 months of age) during other months of the year. Thus if the peak of the fawning season and date of death are known, the only error in aging of fawns, yearlings, and 2-year-olds (to an age of 28 months) would result from variation in birth dates for individual deer, a source of error of less magnitude probably than individual variations in tooth replacement (see section on "Development of Permanent Incisiform Teeth").

Aging of fetuses from 406 gravid does in Utah through use of a growth curve revealed that 68 per cent of the does were probably bred during a 21-day period and 95 per cent during a 44-day period. These records further indicated an over-all spread of about three months in the breeding season and consequently the fawning season. It seems likely, however, that many of the early- and late-born fawns would fail to survive so that the actual spread in the fawning period for deer whose jaws were collected would be even more restricted. Our field observations of pelage changes during late summer and early fall of several thousand 2- to 4-month-old fawns tend to verify this belief.

Peak of the fawning season for central Utah has been determined with fair accuracy to be mid-June by estimating the birth dates of 546 fawns that were caught and ear-tagged. The age of the average fawn when caught was believed to be 4 to 5 days, and few fawns were caught that exceeded an estimated 10 days of age; hence, the error in establishing the peak of the fawning season is probably slight. Thus with evidence that about 95 per cent of the fawns in Utah are born within a period of plus or minus 22 days from the fawning peak of mid-June, we have assumed for purposes of this study that fawns killed in January, for example, are about 7 months old and yearlings about 19 months, etc.

DEVELOPMENT OF PERMANENT INCISIFORM TEETH

Incisiform teeth of mule deer fawns at birth were not examined; but when checked a few hours after, all were found protrud-

TABLE 2. – TOOTH DEVELOPMENT AND REPLACEMENT RECORDS FOR KNOWN-AGE MULE DEER USED IN THIS STUDY, SPECIMENS 4 DAYS TO 33 MONTHS OF AGE AT DEATH, EXAMINED AND/OR EAR-TAGGED WHEN 1 TO 20 DAYS OF AGE [1]

Age at Death		Specimen		Tooth Development and Replacement [2]										
				Incisors			Canines	Premolars			Molars [3]			
Mos.	Days	Number	Sex	1	2	3	1	2	3	4	1	2	3	4
–	4	——	F	m	m	m	m	m	m	(4)	——	——	——	——
–	7	——	F	m	m	m	m	O	m	m	——	——	——	——
–	14	——	M	m	m	m	m	O	m	m	——	——	——	——
4	6	726	F	M	M	M	M	M	M	M	7.1	——	——	——
4	11	A-10	M	M	M	M	M	M	M	M	7.1	——	——	——
4	15	714	M	M	M	M	M	M	M	M	7.4	——	——	——
6	15	Babe's Fawn	M	M	M	M	M	M	M	M	8.7	——	——	——
15	27	2943	F	A	a	O	M	M	M	M	10.6	10.4	——	——
15	28	1599	M	A	A	A	A	M	M	M	12.2	12.0	(2)	——
15	29	2921	F	A	A	a(R) M(L)	O(R) M(L)	M	M	M	9.1	9.6	(2)	——
16	?	423	M	A	A	A	a	M	M	M	10.8	11.5	(2)	——
16	1	2971	F	A	A	A	O	M	M	M	10.4	10.6	(2)	——
16	2	1882	F	A	a(R) M(L)	M	M	M	M	M	10.8	10.3	——	——
16	2	1081	F	A	A	A	a	M	M	M	10.0	11.0	(2)	——
16	2	2596	M	A	a(R) M(L)	M	M	M	M	M	11.6	12.8	(2)	——
16	2	1876	M	A	A	O(R) a(L)	M	M	M	M	10.4	10.2	——	——
16	3	60	M	A	A	a	a	M	M	M	10.4	10.0	——	——
16	4	2965	M	A	A	A	A	M	M	M	11.0	14.1	4.0	——
16	5	2563	M	A	a	M	M	M	M	M	10.6	11.6	——	——
16	6	1091	M	A	a	M(R) O(L)	M(R) O(L)	M	M	M	10.6	10.0	——	——
16	7	2999	M	A	A	A	A	M	M	M	11.2	11.8	(2)	——
16	7	2567	M	A	A	a(R) M(L)	M	M	M	M	11.2	11.6	(2)	——
16	7	2581	M	A	A	a	a	M	M	M	10.8	11.5	(2)	——
16	7	1596	M	A	A	A	a	M	M	M	11.0	12.0	(2)	——
16	8	4009	M	A	A	A	A	M	M	M	9.6	10.6	——	——
16	9	2133	M	A	A	O(R) a(L)	M	M	M	M	9.4	11.4	4.4	——
16	9	1884	M	A	A	a(R) M(L)	O	M	M	M	10.4	11.8	(3)(R) (2)(L)	——
16	9	2998	F	A	A	a	O	M	M	M	9.8	10.8	——	——
16	10	2552	M	A	A	a	O(R) M(L)	M	M	M	10.8	10.9	(2)	——
16	11	4015	M	A	a	M	M	M	M	M	10.7	9.9	——	——
16	12	4037	M	A	A	A	A	M	M	M	10.8	11.9	(2)	——
16	12	1868	M	A	A	A	a	M	M	M	10.4	10.7	(1)	——
16	12	2978	M	A	A	a	M	M	M	M	11.3	13.3	(2)	——
16	12	1842	M	A	A	A	a	M	M	M	10.6	13.2	5.2	——
16	13	1505	F	A	A	a	a	M	M	M	10.0	10.8	——	——
16	15	4030	M	A	A	M(R) O(L)	M	M	M	M	10.3	11.5	(2)	——
16	15	62	M	A	A	a(R) O(L)	O(R) M(L)	M	M	M	11.8	9.3	——	——
16	15	2910	M	A	a	M	M	M	M	M	10.3	12.1	(2)	——
16	16	767	M	A	A	A	a	M	M	M	9.4	11.5	(2)	——
16	16	4089	M	A	A	A	a	M	M	M	10.1	11.6	(2)	——

(Continued on next page)

TABLE 2. — CONTINUED

Age at Death Mos.	Age at Death Days	Specimen Number	Sex	Tooth Development and Replacement[2]										
				Incisors			Canines	Premolars			Molars[3]			
				1	2	3	1	2	3	4	1	2	3	4
16	16	2942	F	A	A	A	A	M	M	M	10.2	10.8	(2)	—
16	17	793	M	A	a	M	M	M	M	M	10.4	10.9	—	—
16	18	774	M	A	M	M	M	M	M	M	9.6	11.0	—	—
16	19	2546	M	A	A	A	a	M	M	M	10.4	11.8	4.0	—
16	20	3072	M	A	a(R) O(L)	M	M	M	M	M	9.6	9.8	(2)	—
16	22	4291	M	A	A	A	M	M	M	M	10.3	12.8	(2)	—
16	23	775	M	A	A	A	a	M	M	M	10.8	13.2	6.2	—
16	23	4002	M	A	A	A	a	M	M	M	11.0	12.8	—	—
19	?	409	F	A	A	A	A	M	M	M	10.2	12.1	7.8	2.5
21	20	2559	M	A	A	A	A	M	a(R) M(L)	M	11.8	13.2	7.6	2.8
28	?	1088	F	A	A	A	A	M	A	A	10.5	13.8	11.4	4.9
28	?	113	M	A	A	A	A	A	A	A	9.8	12.6	12.6	6.7
28	4	2536	M	A	A	A	A	A	A	A	8.2	11.6	12.9	7.9
28	4	1579	M	A	A	A	A	A	A	A	10.9	13.8	8.8	4.7
28	8	2510	F	A	A	A	A	A	A	A	10.5	12.6	11.6	5.9
28	8	768	F	A	A	A	A	A	A	A	10.3	12.7	10.4	3.9
28	9	1520	M	A	A	A	A	A	A	A	10.9	12.7	12.8	7.1
28	9	73	M	A	A	A	A	A	A	A	8.7	10.5	9.5	5.0
28	10	2905	M	A	A	A	A	A	A	A	8.5	11.1	9.8	5.2
28	11	2514	M	A	A	A	A	A	A	A	9.7	12.8	11.8	7.9
28	12	2957	M	A	A	A	A	A	A	A	8.2	12.5	8.7	3.7
28	14	747	M	A	A	A	A	A	A	A	8.4	11.6	9.8	3.7
28	14	756	M	A	A	A	A	A	A	A	9.5	12.5	10.0	5.5
28	15	1592	M	A	A	A	A	A	A	A	9.5	12.8	10.0	6.0
28	17	735	M	A	A	A	A	A	A	A	8.4	12.1	10.5	6.1
28	18	2989	F	A	A	A	A	A	A	A	9.6	12.2	10.0	3.7
28	18	3068	F	A	A	A	A	A	A	A	8.5	11.3	11.6	4.2
30	?	Colo.	M	A	A	A	A	A	A	A	8.3	10.8	11.4	7.5
32	?	2508	F	A	A	A	A	A	A	A	9.7	12.3	10.8	4.6
33	?	Colo.	F	A	A	A	A	A	A	A	7.2	10.0	10.7	5.4

[1] Three specimens included in this table (No. 1088—28 months, Colo. 30 and 32 months) were not ear-tagged until 5 to 10 months of age.

[2] Designation "m" is for partially erupted and "M" for fully erupted milk teeth; "a" and "A" for partially and fully erupted permanent teeth respectively.

"O" indicates the condition where the milk tooth has been lost but the permanent tooth has not yet erupted, or in the case of young fawns where the milk tooth has not yet erupted.

"(R)" and "(L)" indicate right and left side of the jaw where the tooth eruption pattern differed.

[3] Decimal numbers for the molars are average heights of the lingual crests in mm. above the gum line. For M_3, the value is the average height of the anterior and middle cusps while M_4 is the measurement for the posterior cusp of M_3. If all lingual cusps of a molar had erupted, a measurement was taken. If not, the number of points (both buccal and lingual) showing through the gum is listed as a whole number within brackets.

ing through the gums. The average fawn retains the temporary incisors until it is about a year of age, although the first or middle pair of permanent incisors may erupt as early as 11 months in captive animals and possibly in some wild ones, too.

In Table 3 are listed records showing the period of incisor and canine ("corner incisors") replacement for mule deer in Utah (see Riney, 1951, for tooth terminology).

Several hundred jaws from 7- to 10-month-old fawns have been examined, and all possessed temporary incisiform teeth (Table 3). The sample of May (11-month-old) specimens from the wild is limited—only nine—but they too possessed all milk incisiform teeth, and only two of nine 12-month-old deer (examined in June) had any permanent incisors. However, all July specimens (13) had started replacement. From

TABLE 3. — NUMBER OF DEER EXAMINED BY TOOTH AND AGE CLASSES TO SHOW REPLACEMENT PATTERN OF INCISIFORM TEETH IN MULE DEER OF UTAH

Month Examined	Age Mos.	Number Permanent Incisiform Teeth									Total Deer	Mean No. Incisors	Mean Date
		0	1	2	3	4	5	6	7	8			
January-March	7-9	504	—	—	—	—	—	—	—	—	504	—	—
April	10	22	—	—	—	—	—	—	—	—	22	—	—
May	11	9	—	—	—	—	—	—	—	—	9	—	—
June	12	7	—	2	—	—	—	—	—	—	9	0.44	6/15[1]
July	13	—	1	11	—	1	—	—	—	—	13	2.08	7/22
August	14	—	—	21	1	5	1	—	—	—	28	2.50	8/8
September	15	—	—	112	10	77	5	18	1	7	229	3.21	9/25
October	16	1	1	68	49	420	84	266	51	305	1,247	5.45	10/23
January	19	—	—	—	—	4	2	11	5	82	104	7.52	1/10
February	20	—	—	—	—	—	1	2	2	35	40	7.78	2/14[1]
March	21	—	—	—	—	—	1	4	3	165	173	7.92	3/15[1]
April	22	—	—	—	—	—	1	1	—	39	41	7.88	4/15[1]
May	23	—	—	—	—	—	—	—	—	12	12	8.00	5/7[1]
July-Sept.	25-27	—	—	—	—	—	—	—	—	170	170	8.00	—
October	28	—	—	—	—	—	—	—	1	906	907	—	—

[1] The mean date has been approximated because the exact date of death was not known for a few specimens.

this we suppose that most mule deer in Utah are about 12 to 13 months of age before incisor replacement starts. Fig. 1, derived from data in Table 3, indicates a replacement rate of one pair of incisiform teeth about every two months. The reader will note that the Antimony data (15-month-old deer) have not been used in deriving the curve because poor nutrition was suspected of adversely affecting replacement (see "Factors Influencing Tooth Wear and Eruption").

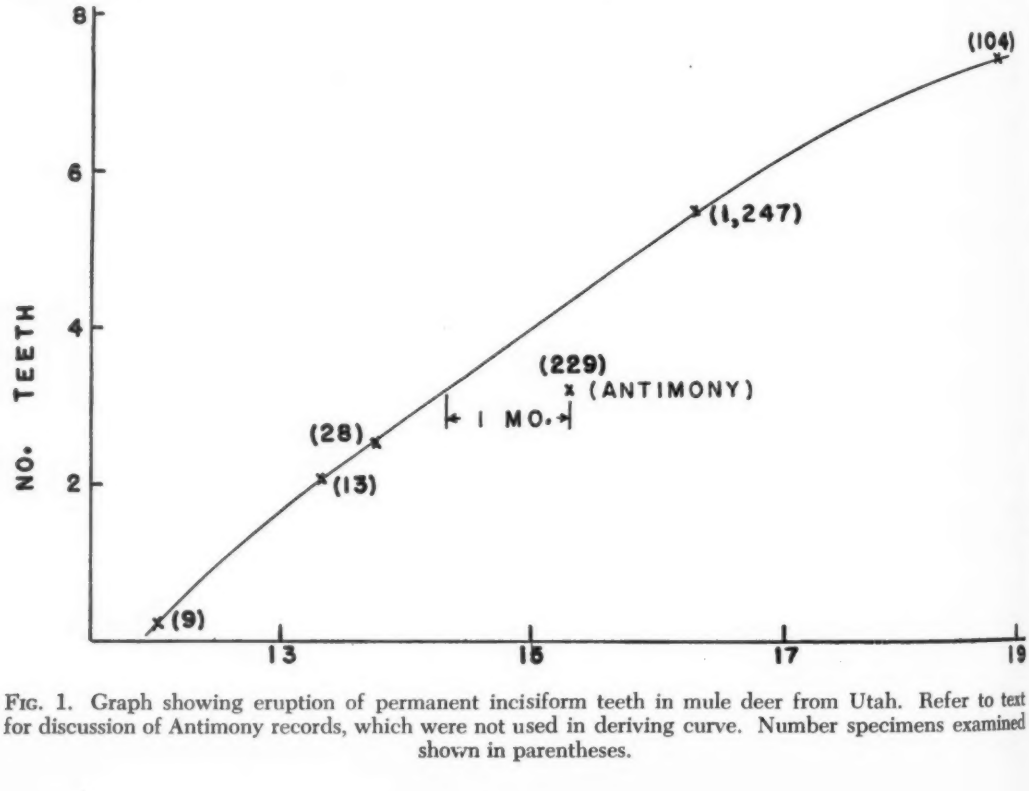


FIG. 1. Graph showing eruption of permanent incisiform teeth in mule deer from Utah. Refer to text for discussion of Antimony records, which were not used in deriving curve. Number specimens examined shown in parentheses.

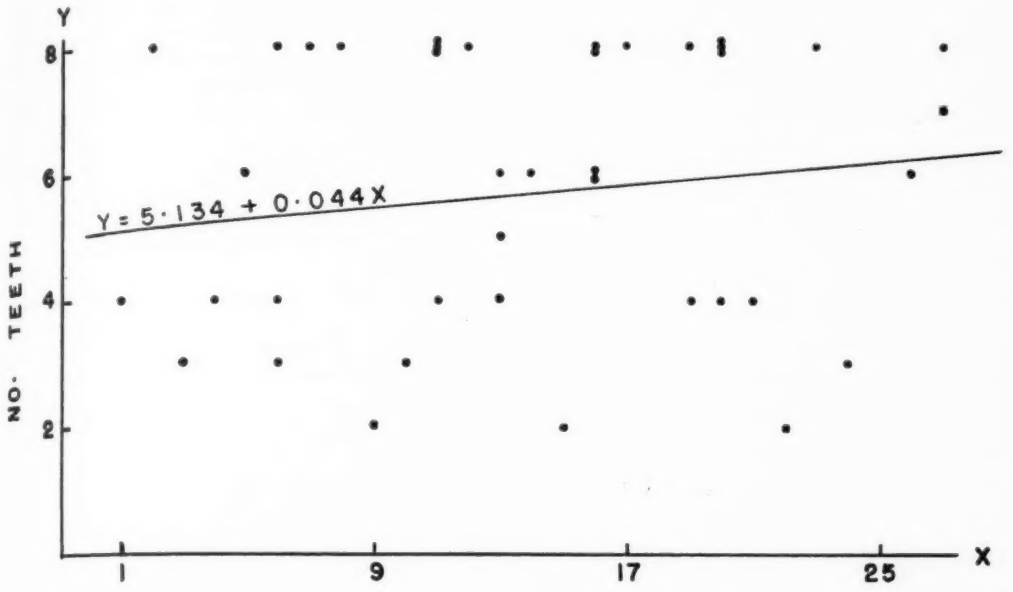


FIG. 2. Regression of number of permanent incisiform teeth on age for 40 known-age yearling mule deer from Utah.

The regression equation $Y = 5.134 + 0.44\,X$ (Fig. 2) represents the replacement rate as displayed by 40 ear-tagged yearlings killed by hunters where Y is the number of permanent incisiform teeth and X the number of days in excess of 483 days of age. Ages of the deer varied from 484 days (1 yr., 3 mos., 27 days) to 510 days (1 yr., 4 mos., 23 days). The equation indicates a replacement rate of a pair every 46 days, which differs from the approximately two-months' period derived from the more generalized curve of Fig. 1.

Observations of a live experimental deer at Logan, Utah, indicate a 2-month interval between eruption of the first and second pairs of permanent incisors. When the 11-month-old fawn was first examined on May 21, it had one pair of half-erupted permanent incisors. When re-examined July 20 (2.3 months later), it had two pairs of almost fully erupted permanent incisors.

Four additional 11- to 12-month-old captive deer were examined at the Yountsville Game Farm through courtesy of California Fish and Game Department personnel. These observations showed that Columbian black-tailed deer (*O. h. columbianus*) and Rocky Mountain mule deer may have a similar pattern of incisor eruption and suggested that the incisors of captive deer in good condition may erupt a little sooner than in wild animals. One black-tailed deer had all milk incisiform teeth, while another had one pair of half-erupted incisors. A Rocky Mountain mule deer fawn had one pair of half-erupted incisors while a hybrid between the two subspecies retained all milk incisors. Thus of five 11- to 12-month-old captive deer that we have examined, three had erupted their first pair of permanent incisors in contrast to only 2 of 18 wild deer. It is possible that the captive deer enjoyed a superior overwinter diet, thereby promoting earlier eruption. Because of this possibility, captive animal records have been excluded from Table 3.

We have examined only one yearling during the October hunt (average age of yearlings—16 months) that had no permanent incisors. This individual had five heavily worn milk incisors, while all the permanent incisiform teeth appeared impacted, giving a lumpy appearance to the anterior portion of the mandibles.

Despite the variations noted above, it appears that eruption of permanent incisors in Rocky Mountain mule deer generally

commences at about 12 to 13 months of age and that replacement thereafter is at the approximate rate of a pair every 1 1/2 to 2 months with eruption (including canines) complete at 18 months. Similarly, Cowan (1936) states that permanent incisors first erupt in Columbian black-tailed deer at the age of about one year with eruption usually complete at the age of 18 months. Similar findings have been reported by Jones (1953) for the Inyo mule deer (*O. h. inyoensis*). Also Hunter (1947) reports that the first incisors are cut in Rocky Mountain mule deer of Colorado when the deer is about one year old, while the remaining incisiform teeth may be cut between the ages of 12 and 16 months. Leopold, *et al.* (1951), however, report a more variable incisor eruption for California mule deer (*O. h. californicus*), with eruption of the first pair of permanent incisors occurring between the ages of 5 and 18 months. Moreland (1952) differs with Cowan in reporting eruption of the first pair of permanent incisors in Columbian black-tails at six months and a "full mouth" at 12 months, but a possibility of error exists inasmuch as Moreland attempted to apply Severinghaus' (1949) whitetail findings to the blacktail. Severinghaus (1949) reports initial eruption of permanent incisors at 5 months in the white-tailed deer with a "full mouth" at 11 months.

Many individual differences exist in incisor eruption as demonstrated by our known-age material. Thus, one yearling (No. 774) 505 days of age (1 yr., 4 mos., 18 days) at death had but a single pair of permanent incisors, whereas another (No. 1599) 20 days younger had a "full mouth." The two deer ranged during the entire period within the same township (six miles square). Allowing 1.5 to 2 months for eruption of each pair of incisiform teeth, one would suspect that the one deer may have been 4.5 to 6 months older than the other, rather than 20 days younger. Although this is our most exaggerated case among known-age specimens, there are nevertheless many instances where individual deer have had fewer permanent front teeth than others of the same age or younger (Table 2).

Records in Table 3 likewise indicate several months' variation of incisor replacement. One yearling examined in September (probably 15 months of age) had a "full mouth," whereas at the other extreme are two yearlings examined as late as April (probably 21 months of age) that had not yet attained all permanent incisiform teeth and even one 28-month-old buck that had but seven incisiform teeth. The eighth tooth of the latter animal was found heavily encased in bone, and eventual eruption was in question.

PREMOLAR DEVELOPMENT

We have but three observations of premolar development in young fawns at or shortly after birth. The premolars of a 4-day-old fawn had all erupted except the posterior crown of P_4 (third premolar) of the left mandible, which was still covered by membrane. Another fawn about a week old had erupted all premolars except P_2 on both sides. The third fawn was about two weeks old, and the first premolars (P_2) of each mandible had likewise not erupted, even though their counterparts in the maxillas had. This particular animal, however, was a "parrot-mouth" having a shortened mandible, so impaction and hence delay in tooth eruption may have resulted.

TABLE 4. — PREMOLAR REPLACEMENT IN MULE DEER OF UTAH

Month	Approx. Age of Deer in Months	Number of Deer Examined (% in parentheses) Status of Milk Premolars			Total
		All Present	Partly Shed	All Shed	
January	19	36 (100)			36
February	20	40 (98)	1 (2)		41
March	21	196 (94)	13 (6)	1	210
April	22	34 (83)	7 (17)		41
May	23	17 (63)	8 (30)	2 (7)	27
July	25	0	1 (50)	1 (50)	2
August	26	0	2 (25)	6 (75)	8
September	27	1 (1)	10 (6)	149 (93)	160
October	28	0	5 (1)	902 (99)	907

Milk premolars are retained until the average deer is about two years of age, but there is considerable variation. We have noted loss of some milk teeth as early as February (20-month-olds) (Table 4) and retention as late as October (28 months). However, most of the replacement apparently occurs when the deer are 22 to 26 months of age with a peak of 24 months (Table 4 and Fig. 3).

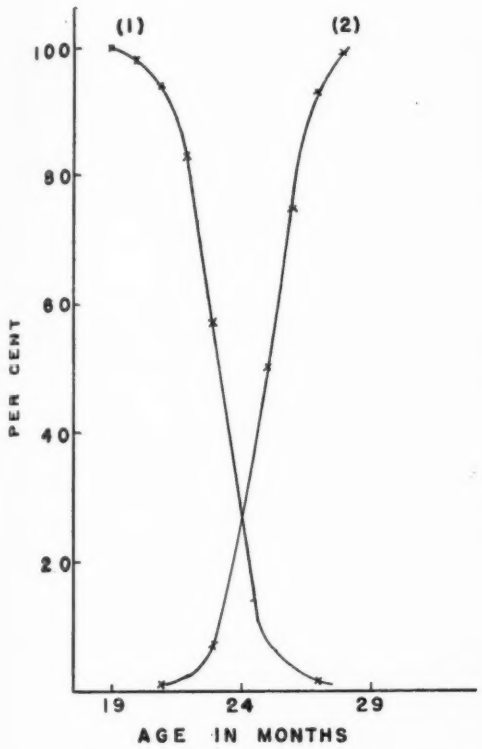


FIG. 3. Premolar replacement pattern in mule deer of Utah—from Table 4: (1) percentage of specimens having all temporary milk premolars; (2) percentage having all permanent premolars.

Our findings agree well with Jones (1953) for Inyo mule deer but disagree with Cowan (1936) for Columbian blacktails where eruption of P_4 was found to occur at 18 to 20 months of age, with eruption of the others following; with Leopold, *et al.* (1951), whose findings with California mule deer concurred with Cowan's (1936) for the Columbian blacktails; and with Hunter (1947), who reported premolar shedding at 30 to 32 months of age and in some instances not until 40 months among Rocky Mountain mule deer.

DEVELOPMENT AND WEAR OF THE MOLARS

We believe that wear of the molars offers the best means of aging mule deer older than two years and for this reason are giving a more comprehensive discussion of development and wear of molars than for the other teeth.

Photographs (Pl. 1 to 4) of the molariform teeth of mandibles from known-age deer are also given, providing a visual means of associating tooth development and wear with age.

In Table 5 are shown the approximate ages at which each of the molars first erupt. Points of M_1 first appeared in 2.5- to 3.5-month-old fawns with eruption apparently completed in 12- to 14-month-old deer. Points of M_2 appeared first in 8-month-old specimens, and the tooth appears fully erupted at 20 to 23 months. Points of the anterior and middle cusps of M_3 first emerge in 15-month-old animals, and the tooth appears fully erupted in 2-year-4-month-old deer. However, the line of demarcation is not clearly defined because of sampling variation. The posterior cusp of M_3 first was evident in 1-year-7-month-old deer. It is possible, however, that this cusp could appear one or two months sooner inasmuch as we examined no specimens 1 year and 5 to 7 months old.

Table 6 shows the average height of the lingual crests of each molar above the gum line for deer of different ages. Tooth height alone may adequately express wear and hence approximate age for deer of a fairly constant stature. However, members of the different subspecies of *Odocoileus hemionus* vary considerably in stature and tooth size so that a more generally acceptable expression of tooth wear seems desirable. As a consequence we have used the ratio between the sum of widths of the seven occlusal surfaces on the buccal side and the sum of the heights above the gum line of the corresponding lingual crests. The sum of the wearing-surface measurements has been divided by the height measurements so that the ratio increases with age of the animal.

(Text continued on page 146)

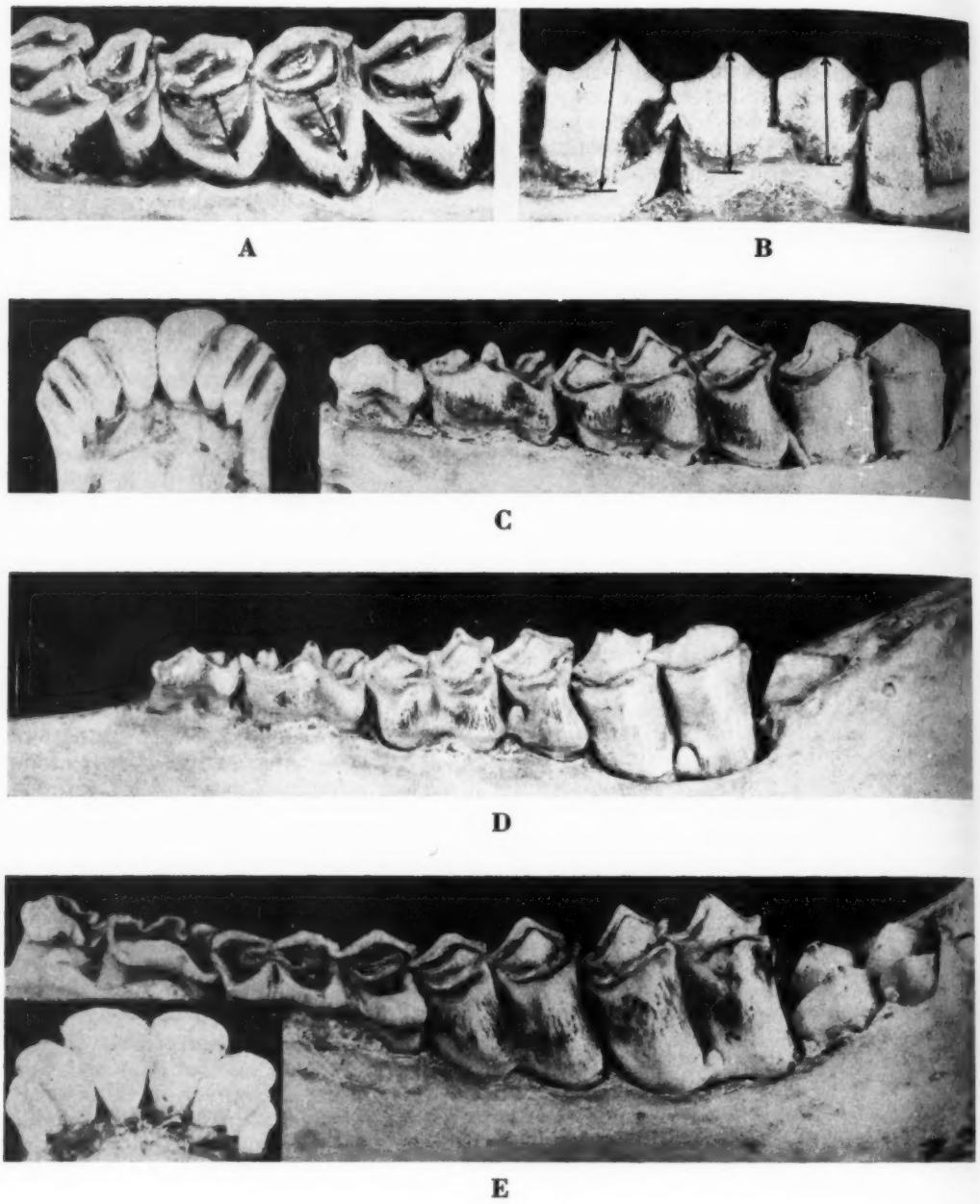


PLATE 1. TEETH OF ROCKY MOUNTAIN MULE DEER

A. Surfaces of M_1 and anterior crown of M_2 showing occlusal surface measurements taken of buccal crowns.
B. View of lingual side of M_1 and anterior crown of M_2 showing measurements taken of crest heights.
C. Milk incisiform teeth and cheek teeth of 4-month-old fawn.
D. 6.5-month-old.
E. Incisiform teeth—two pairs of permanent and two pairs of temporary teeth—and cheek teeth of a 1-year-4-month-old.

A

B

C

D

PLATE 2. TEETH OF ROCKY MOUNTAIN MULE DEER

A. 1-year-7-month-old.
B. 1-year-10-month-old.
C. 2-year-4-month-old.
D. 3-year-4-month-old.

A

B

C

D

PLATE 3. TEETH OF ROCKY MOUNTAIN MULE DEER

A. 4-year-4-month-old.
B. 5-year-4-month-old.
C. 8-year-3-month-old.
D. 9-year-4-month-old.

A

B

C

D

PLATE 4. TEETH OF ROCKY MOUNTAIN MULE DEER

A. 10-year-6-month-old.

B. Possible 15-year-old.

C. Possible 16-year-old or older.

D. Incisiform and cheek teeth of a 2-year-7-month-old deer afflicted with fluorosis. Note pitting of middle pair of incisors and broken condition of the second and third pairs; also note eroded condition of cheek teeth (except M_1) and irregular wear of P_3, P_4, M_2, and M_3.

TABLE 5. — MOLAR ERUPTION AMONG MULE DEER OF UTAH AND COLORADO

Month of Death	Approx. Age		Number Specimens	Points of Molars Showing through Gums										
				None				Part			All			
				Molar No.				Molar No.			Molar No.			
	Years	Mos.		1	2	3[1]	4[1]	1	2	3	1	2	3	4
				(Percentage of Specimens Examined)										
July	—	1	1	100	—	—	—	—	—	—	—	—	—	—
August	—	2	2	50	—	—	—	50	—	—	—	—	—	—
September	—	3	6	50	—	—	—	50	—	—	—	—	—	—
October	—	4	10	—	—	—	—	—	—	—	100	—	—	—
January	—	7	9	—	100	—	—	—	—	—	100	—	—	—
February	—	8	61	—	74	—	—	—	26	—	100	—	—	—
March	—	9	233	—	43	—	—	—	50	—	100	7	—	—
April	—	10	23	—	17	—	—	—	52	—	100	31	—	—
May	—	11	4	—	—	—	—	—	50	—	100	50	—	—
June	1	0	5	—	—	—	—	—	20	—	100	80	—	—
July	1	1	13	—	—	—	—	—	—	—	100	100	—	—
August	1	2	27	—	—	—	—	—	—	—	100	100	—	—
September	1	3	22	—	—	45	—	—	—	55	100	100	—	—
October	1	4	44	—	—	36	—	—	—	52	100	100	12	—
January	1	7	19	—	—	—	68	—	—	11	100	100	89	32
February	1	8	23	—	—	—	44	—	—	—	100	100	100	56
March	1	9	201	—	—	—	23	—	—	—	100	100	100	77
April	1	10	39	—	—	—	22	—	—	—	100	100	100	78
May	1	11	9	—	—	—	33	—	—	—	100	100	100	67
July-Oct.	2	1-4	24	—	—	—	—	—	—	—	100	100	100	100

[1] No. 3 pertains to the anterior and middle crowns of M_3 of the mandibles and No. 4 refers to the posterior crown of M_3.

Measurements of the occlusal surfaces were taken with calipers to the nearest tenth of a mm. from the outer edge of the infundibulum radially across the widest part of each crown to the outer edge of the wearing surface (Pl. 1, A). Accuracy in these measurements, however, diminishes in the older specimens because the infundibula are frequently worn away. Height measurements of the lingual crests were taken from the gum line to the highest point of each crown (Pl. 1, B). Unless a noticeable variation in tooth wear existed, measurements were taken only of teeth in the left mandible; otherwise values for both mandibles were averaged.

Although we independently developed the idea of expressing tooth wear as a ratio, originality cannot be claimed because Passmore, *et al.* (Peterson, 1955—Appendix A) employed a similar type ratio for moose, using measurements of the posterior buccal crown of M_2. It is probable that others have also used ratios to express tooth wear.

The ratios have been plotted in Fig. 4 and a curve drawn for known-age deer, 28 months of age and older. Extension of the curve beyond the age of 9 years, 4 months was accomplished after the method of Passmore, *et al.* (Peterson, *ibid.*). A few unknown-age jaws showing more tooth wear than the known-age 9-year-old were selected and placed in wear classes. Ratios derived from their molar measurements were then plotted on the graph (Fig. 4). Each age class from 10 to 16 years was represented, resulting in a smooth ascending curve. The highest ratio obtained was 1.51 with an indicated age of 16 years. Average ratios derived from the curve are listed in Table 7 for each age class. Four jaws gave the appearance of being older than the ones judged as 16-year-olds from Fig. 4, and yet the tooth ratios indicated they were from younger deer. The molars of one of these jaws (Pl. 4, C) were so badly worn that the two crowns of M_1 and M_2 had separated, as had the anterior and middle crowns of M_3. When a tooth is worn down to the cervix, width of the occlusal surface diminishes seemingly at a faster rate than the tooth height. If this condition actually occurs in very old animals, the curve should turn downward in Fig. 4 after 16 years. If such is the case, age of the four deer mentioned previously may have exceeded 16 years.

TABLE 6. — MOLAR DEVELOPMENT AMONG MULE DEER OF UTAH AND COLORADO

Month of Death	Age Yrs.	Age Mos.	No. Specimens	Molars–Hgt. above Gum Line (mm.) 1	2	3[1]	4[1]
September		3	6	2.0	—	—	—
October		4	10	6.0	—	—	—
January		7	9	10.1	—	—	—
February		8	39	10.3	—	—	—
March		9	42	9.8	0.5	—	—
April		10	23	10.3	1.3	—	—
May		11	4	9.9	2.9	—	—
June	1	0	3	10.8	4.8	—	—
July	1	1	12	10.7	9.8	—	—
August	1	2	27	10.9	9.7	—	—
September	1	3	10	10.6	11.1	—	—
October	1	4	44[2]	10.6	11.3	0.5	—
January	1	7	19	10.1	11.5	6.2	0.6
February	1	8	23	10.3	12.7	7.9	1.3
March	1	9	34	9.6	11.5	7.5	1.6
April	1	10	39	9.7	12.0	7.9	2.1
May	1	11	9	10.3	12.8	8.1	2.0
July	2	1	1	10.2	12.8	10.2	3.0
August	2	2	6	10.0	11.6	8.9	3.5
September	2	3	3	10.2	12.9	10.4	5.5
October	2	4	17[2]	9.6	12.3	10.7	5.4
January	2	7	1[2]	8.3	10.8	11.4	7.5
February	2	8	1[2]	9.7	12.3	10.8	4.6
March	2	9	1[2]	7.2	10.0	10.7	5.4
August	3	2	1[2]	9.5	11.6	12.5	6.3
October	3	4	5[2]	8.6	10.9	11.0	6.0
October	4	4	4[2]	7.7	10.4	10.9	6.6
April	4	10	1[2]	6.6	10.8	11.2	6.5
October	5	4	2[2]	7.6	10.2	11.0	6.2
September	8	3	1[2]	6.2	9.3	8.3	6.6
October	9	4	1[2]	6.0	8.2	8.8	6.5

[1] No. 3 pertains to the anterior and middle crowns of M_3 whereas No. 4 pertains to the posterior crown of M_3.
[2] Tagged deer and hence known-age.

There is limited evidence that individuals of the *Odocoileus hemionus* group attain ages of 15 years and older. Cowan (1936) records an instance of a black-tailed buck reaching the age of at least 16 years. Frank Golley, a graduate student at Washington State College, furnished the writers with photographs of the mandible from a Columbian black-tailed pet doe that was 18.5 years old at death, and biologist Fred Zwickel of the State of Washington Department of Game also kindly furnished photographs of the lower jaw of a mule deer doe known to have been a minimum of 14 years, 9 months. The animal was mature when trapped, tagged, and released in the wild, hence it could well have been older than the established minimum. We not infrequently obtain jaws from hunter-killed mule deer in Utah and Colorado that show as much wear of the molariform teeth as displayed by the Washington specimens. Two such mandibles are shown in Plate 4, B and C. Tooth ratios of 1.25 and 1.31 were respectively derived for these two specimens, with indicated ages of 15 years 4 months and 15 years 7 months. Because of crown separation in each of the molars, we feel the latter animal (Pl. 4, C) could be two or three years older than the former rather than merely a few months, for reasons discussed previously.

Molar measurements of three jaws from known-age deer were not used in deriving the ratios of Fig. 4 and Table 7 because of atypical wear. Two jaws were from captive deer where type of food may have influenced tooth wear. One of these deer was a buck 4 years and 9 months old at death. He

FIG. 4. Graph showing relation of molar tooth ratios (sum of widths of all buccal crests/sum of lingual heights) to age for mule deer of Utah and Colorado.

TABLE 7. — MOLAR TOOTH RATIOS FOR DIFFERENT AGE CLASSES AS DERIVED FROM FIG. 4

Age		Molar Ratio	95 Per Cent Confidence Limits[1]
Years	Months		
2	4	0.33	0.11 - 0.45 (16)
3	4	0.40	0.19 - 0.61 (5)
4	4	0.45	0.29 - 0.61 (4)
5	4	0.50	0.23 - 0.77 (2)
6	4	0.54	
7	4	0.58	
8	4	0.62	
9	4	0.67	
10	4	0.73	
11	4	0.80	
12	4	0.88	
13	4	0.97	
14	4	1.10	
15	4	1.25	
16	4	1.46	

[1] Limits listed only for those classes containing two or more known-age jaws; number of specimens given within brackets.

had been reared largely on garbage, and tooth wear was substantially less than wild deer of similar age. The other captive deer was a 10.5-year-old buck (Pl. 4, A). Wear of its molars was much as might be expected (as based on the known 8-year-3-month- and 9-year-4-month-old deer) insofar as buccal tooth heights and absence of infundibula in both crowns of M_1 were concerned. Wear differed, however, in the low lingual crests and relatively flat occlusal surfaces. As a consequence, the tooth ratio of 1.60 exceeded any thus far obtained even for individuals obviously much older. Type of feed —principally rolled oats and alfalfa hay— may have influenced wear. The incisors, through relative nonuse, were scarcely worn.

The third rejected jaw was from a wild 5-year-4-month-old buck where molariform teeth showed normal wear, except for the

first molar of each mandible. Wear had been so heavy on these two teeth that no infundibula remained and in this respect exceeded that of the known 8- and 9-year-olds and more nearly resembled the 10.5-year-old. The unusual wear appeared directly attributable to malposition of the first molars; each was offset 2.5 mm. from the lingual margin of the tooth row. Because of heavy wear of M_1 the molar-tooth ratio was raised to 0.60, which is what might be expected in a 7.8-year-old (Fig. 4). It is well to recognize that deviations of this magnitude exist, but we feel this jaw should not be used in Fig. 4 until a greater number of specimens are obtained in the age classes above four years.

SUMMARY OF TOOTH ERUPTION AND REPLACEMENT

A summary of tooth development and replacement records is listed in Table 8. It might be mentioned that, at the time of the fall hunting season, inexperienced workers sometimes mistake the middle pair of temporary incisors in 4-month-old fawns as permanent teeth because the middle pair is larger and of a different shape than its contemporaries. Photographs of the incisiform teeth of a fawn and yearling (Pl. 1, C and E) point out the differences between the middle pair of milk and permanent incisors. At the time of the October hunting season, most yearlings are in the process of replacing the temporary incisors. However, one yearling in four or five may have acquired all permanent incisiform teeth. These individuals differ from fawns or 2-year-olds, however, by having heavily worn milk premolars with M_1 and M_2 fully erupted, and M_3 may or may not have erupted. A fawn has little-worn milk premolars, and only M_1 of the molars has erupted. Essentially all 2-year-olds have newly erupted premolars that consequently show little wear and frequently lighter staining than the molars; also M_3 is fully erupted but the posterior crest shows only slight wear. Two of our 17 known-age 28-month-old deer, however, showed no wear on the posterior cusps of M_3.

No written description of tooth wear for the different age classes is being attempted. The photographs and molar tooth ratio, we believe, give a more satisfactory portrayal. It does appear that not only tooth eruption but wear as well may be delayed in Rocky Mountain mule deer over that reported for white-tailed deer (Severinghaus, 1949).

TABLE 8. — SUMMARY OF TOOTH REPLACEMENT AND DEVELOPMENT IN MULE DEER OF UTAH AND COLORADO

Tooth Development and Replacement	Period of Occurrence (Age in Months)	
	Average	Range
Incisiform teeth		
Milk incisors through gums	At birth	
First pair permanent incisors fully erupted	12-13	11-16
Second pair permanent incisors	14-15	13-18
Third pair permanent incisors	16-17	15-22
Canines ("corner incisors")	17-18	15-28
Premolars		
Milk teeth lost	24	20-28
Permanents fully erupted	25	21-29
Molars		
1st (points first showing)	3	2.5-3.5
(fully erupted)	12	8-16
2nd (points first showing)	10	8-12
(fully erupted)	20	15-25
3rd (points first showing)	16	15-19
(fully erupted)	28	25-30(?)

FACTORS INFLUENCING TOOTH WEAR AND ERUPTION

Fluorosis

Unquestionably many factors govern the rate of wear in deer teeth. One of these is fluorosis involving hundreds of deer in the mountains east and northeast of Orem, Utah. Source of the fluorine has been fumes given off by a near-by steel plant. Fluorine may occur not only in industrial wastes but also in concentrated amounts in the soil and water of certain areas as well. Chemical analysis of the premolars of a 2-year-old buck with affected teeth from the Orem area showed a high level of 1,500 p.p.m. of fluorine.

Fluorine has a marked affinity for calcium and excessive quantities interfere with normal calcification in the bones and teeth. Teeth afflicted by fluorosis are characteristically pitted and mottled. The enamel is sometimes chalky in appearance but is frequently heavily stained. Because the enamel is soft and brittle, wear is rapid and irregular. Selective abrasion often results in unevenness of crown level in the cheek teeth (Pl. 4, D). Typically, the first molar (M_1) appears normal, as do all temporary teeth. Fluorine affects only those teeth that are in

the formative stage at the time toxic amounts are ingested. Toxic amounts of fluorine in domestic livestock are apparently not passed from the mother to the developing fetus nor to the young after birth through the mother's milk (Agate, *et al.*, 1949). For this reason the milk teeth and first molars of deer are usually unaffected, because these teeth are fully erupted or formed before the animal has had an opportunity to build up a toxic dosage of fluorine in the body.

Aging of deer older than 2.5 years that are affected with severe fluorosis is a hazardous undertaking.

Nutrition

Franklin (1950) has shown through experimental feeding of sheep in Australia that faulty nutrition—deficiency of calcium and a wide calcium-phosphorus ratio—may create tooth abnormalities similar to those of fluorosis. Other irregularities noted by Franklin were delayed tooth eruption, failure of teeth to erupt in extreme cases, and abnormal angles at which teeth erupted.

We have encountered some evidence among deer that a lowered nutritional plane may delay tooth eruption. We have already mentioned that eruption of permanent incisiform teeth of yearlings killed on the Antimony unit of southern Utah appears to be delayed about one month compared to deer in other parts of the state (Fig. 1). The Antimony range is one of the most severely overused ranges (combined livestock and deer use) in the state, and this observation seems borne out by the low reproductive rates and weights of deer from the area.

Other records indicate that incisor eruption may have been delayed following the two severe winters of 1948-49 and 1951-52 on the Oak Creek unit of central Utah. Yearlings killed in October following the two severe winters had a mean of 5.24 permanent incisiform teeth showing above the gums for 196 animals examined, compared to a mean of 5.71 teeth for 570 deer examined in 1950, 1951, and 1953-55 following moderate winters. The difference in the mean number of teeth is not statistically significant at the 5 per cent level; but it suggests the role nutrition might play in tooth eruption, for unquestionably the nutritional balance is less favorable during severe winters.

Another indicator of the possible influence of nutrition upon tooth eruption is the time of year when most eruption occurs. Our study shows that most of the incisor and premolar replacement and eruption of M_1 and M_2 occurs during late spring, summer, and early fall—the period when food conditions are most favorable. The third molar appears to be the only exception, for most of its eruption occurs from late fall to early spring. Scheffer (1950) reports a seasonal growth in the teeth of fur seals (*Callorhinus ursinus*), apparently conforming to periods of high food intake. A count of the resulting growth rings on the canines gives a fairly accurate estimate of age.

Other Factors

Added study has revealed an increase in hog-dressed weights of yearlings killed by hunters in central Utah with an increase in the number of erupted permanent incisiform teeth (Table 9).

TABLE 9. — HOG-DRESSED WEIGHTS BY INCISOR CLASSES FOR YEARLING DEER KILLED BY HUNTERS IN CENTRAL UTAH

	No. Pairs Permanent Incisiform Teeth				
	1	2	3	4	Total
No. deer weighed					
Bucks	79	391	235	210	915
Does	24	86	70	56	236
Weights (pounds)					
Bucks	85.2	87.7	89.4	91.5	—
Does	75.9	78.7	79.5	81.3	—

Inasmuch as we have already shown a correlation of incisor eruption with age, it would appear that a portion of the variation in incisor eruption with weight could also be due to age. However, with an estimated 95 per cent of the fawns being born within a 44-day period and with 1.5 to 2 months required for eruption of each pair of incisiform teeth, it is apparent from information in Table 8 that individual variation must be a dominant factor. The dentition pattern in this table implies an age spread of 4.5 to 6 months (allowing 1.5 to 2 months per pair of incisiform teeth) for a sizable segment of this age class (about 9 per cent of bucks have one pair and 23 per cent have four pair—Table 9), whereas the actual spread is likely no more than three months (created

by limits of the fawning and hunting seasons) except for a few rare individuals.

An example of individual variation in incisor development apart from age and weight may be found in buck No. 2562 (505 days of age and weighing 98 pounds, hog-dressed) compared to buck No. 4089 (503 days old and 81 pounds). The first buck was not only 17 pounds heavier than the second and two days older but it had only one pair of permanent incisors compared to a complete set of incisiform teeth for the latter. The deer were from the same canyon so that food conditions were similar for both.

One might suspect earlier tooth eruption among does than bucks because of earlier physical maturity of the former. This does not appear to be the case, however. Our data show an average of 5.13 permanent incisiform teeth for 1,178 October-killed yearling bucks from Utah compared to 4.88 for 365 does. The difference is not statistically significant at the 5 per cent level, however, and the relation between the sexes is so variable for different units and years that there is doubt of any real difference.

Ingested grit or sand influences the rate of tooth wear among domestic livestock. The amount of abrasives actually consumed probably varies with soil type, degree of aridity and overgrazing, and amount of exposed soil. Deer could similarly be influenced although likely to a lesser degree, because deer do not usually feed so closely to the ground as livestock. However, the writers have frequently found tiny bits of rock in the infundibula of deers' teeth.

ACCURACY IN AGING DEER

Many big-game workers have expressed doubt as to the value of tooth wear as a means of aging deer. Such doubts seem well justified from Fig. 4 where there is an obvious overlap in molar ratio values of 2-year-olds with 3- and even 4-year-olds; and we have already pointed out that one 5-year-old could be mis-aged as a 7.8-year-old.

Our material is too limited to indicate the overlap to be expected in the older age classes, but in all probability the errors possible in correct aging are even greater. The reader might then question the propriety of deer aging where errors of such magnitude are possible. We feel that the chart offered in Fig. 4 and the photographs of Plates 1 to 4 do not permit positive aging except with rather low probabilities. Their prime use lies in determining percentage composition by age classes of deer killed by hunters or other factors. In age assignments of this kind, where a large number of specimens are involved, the errors should tend to be compensating providing, of course, the aging criteria are representative. We wish to stress, however, that the aging curve presented in this paper is subject to change as added specimens of known age are obtained, especially in the older age classes. The curve might also vary with subspecies of mule deer and with geographic location for a single subspecies.

The primary value of the photographs and aging curve presented in this paper is to assist the user in selecting, tentatively at least, a jaw collection representing the various age classes. Thus, if jaws are removed from hunter-killed deer of unknown age, they can best be aged through a visual side-by-side comparison with jaws of the collection.

ADDENDUM

Since this paper went to press, 14 additional mandibles from known-age deer have been procured in Utah and, although no new age classes are represented, it is believed worth-while to provide data on these new specimens. The new mandibles include two from 4-month-old fawns, three from 16-month-olds, seven from 28-month-olds, and one each from the 40- and 52-month-old classes.

Dentition records for the new specimens are listed in Table 1A where the same symbols and legend are used as in Table 2 of the foregoing paper except that the last column of the present table lists molar ratios for each specimen 28 months of age or older. All molar ratios for new specimens fall within the range of values previously established for each age class (Fig. 4). The average ratio for the new total of twenty-three specimens 28 months old is 0.34 in contrast to 0.33 as indicated by Fig. 4. The final average ratio for six 40-month-old specimens is 0.39 compared to the curve value of 0.40, and for five 52-month-olds the average is 0.46 compared to 0.45 from the curve.

Three of the 23 deer that were 28 months old showed no wear on the posterior crown of M_3, and the average width of the wearing surface on the buccal side (measured radially from the infundibulum to the outer edge of the wearing surface) was only 1.64 mm. (0.0–2.9). The same measurement for the six 40-month-old deer was 2.83 mm. (2.4–3.7).

TABLE 1A. — TOOTH DEVELOPMENT AND REPLACEMENT RECORDS FOR KNOWN-AGE MULE DEER; 4 TO 52 MONTHS OF AGE, EAR-TAGGED WHEN 1 TO 20 DAYS OF AGE[1]

Age at Death		Specimen	Tooth Development and Replacement												
				Incisors			Canines	Premolars			Molars				Molar
Mos.	Days	Number	Sex	1	2	3	1	2	3	4	1	2	3	4	Ratio
4	11	A-185	M	M	M	M	M	M	M	M	7.2	—	—	—	—
4	18	A-186	F	M	M	M	M	M	M	M	9.8	—	—	—	—
16	10	A-203	M	A	A	A	A	M	M	M	9.6	11.9	4.6	—	—
16	13	A-27	F	A	a	M	M	M	M	M	9.8	9.8	—	—	—
16	15	A-29	F	A	A	A	A(R) a(L)	M	M	M	11.2	11.4	(1)	—	—
28	?	A-756	M	A	A	A	A	A	A	A	9.4	12.5	12.6	5.2	0.35
28	3	2144	M	A	A	A	A	A	A	A	12.4	14.6	11.4	4.4	0.29
28	14	4014	M	A	A	A	A	A	A	A	10.4	11.8	8.4	3.0	0.31
28	19	2119	F	A	A	A	A	A	A	A	8.4	11.2	9.4	4.2	0.36
28	19	2120	M	A	A	A	A	A	A	A	9.3	12.6	11.7	4.2	0.35
28	19	4028	M	A	A	A	A	A	A	A	8.8	12.0	10.8	4.3	0.38
28	28	1972	M	A	A	A	A	A	A	A	8.8	10.9	9.4	5.3	0.40
40	12	4019	F	A	A	A	A	A	A	A	8.5	11.1	10.7	5.3	0.42
52	15	4276	F	A	A	A	A	A	A	A	7.0	9.8	10.1	5.3	0.48

[1] Deer No. A-756 was not ear-tagged until it was a yearling.

SUMMARY

A dentition study was made by the writers of the Rocky Mountain mule deer of Utah and Colorado. Material consisted of 91 known-age deer varying from 4 days to 10.5 years of age and supplemented by hundreds of jaws collected from deer of unknown age throughout the year to establish the time and rate of tooth replacement.

Replacement of incisiform teeth commences in the average animal at about 12 months of age or shortly after and is completed about 6 months later. The peak of premolar replacement occurs when the average deer is 24 months of age. The first molar erupts in 3-month-old fawns, the second molar appears at about 9 months, and the third at about 15 months. Wear of the molar teeth is expressed in this paper as a ratio between the sum of the widths of the occlusal surfaces of the buccal crowns and the sum of the heights of the lingual crests.

Several factors may affect rate of tooth replacement and wear and hence introduce errors in aging. Influence of fluorosis, nutrition, type of forage, abrasives and individual variation upon tooth eruption and wear are discussed.

The writers recognize the errors possible in aging individual deer. However, it is felt that the prime value of aging comes from determination of age composition of hunter-killed deer. In this respect, errors should be compensating providing the samples are of adequate size and the aging criteria are representative for the area of study.

LITERATURE CITED

AGATE, J., N., *et al.* 1949. Industrial fluorosis, a study of the hazard to man and animals near Fort William, Scotland. A report to the fluorosis committee. His Majesty's Stationery Office, London, Med. Res. Coun. Memo. No. 22.

ANDERSON, J. 1953. Analysis of a Danish roe-deer population (*Capreolus capreolus* L.) based upon the extermination of the total stock. Danish Rev. Game Biol., 2:127-155.

BANFIELD, A. W. F. 1955. A provisional life table for the barren ground caribou. Canad. J. Zool., 33:143-147.

COWAN, I. McT. 1936. Distribution and variation in deer (Genus *Odocoileus*) of the Pacific Coastal Region of North America. Calif. Fish and Game, 22:155-246.

FRANKLIN, M. C. 1950. The influence of diet on dental development in the sheep. Commonwealth Scien. and Indus. Res. Organ., Melbourne, Australia, Bul. No. 252, 34pp., 23 pl.

GILL, J. 1953. Remarks on the analysis of kill-curves of female deer. Proc. NE. Section Wildl. Soc. 9th Annl. Conf., Bretton Woods, N. H., Sept. 20-23, 1953. 12pp. mimeo.

HAYNE, D. W. AND L. EBERHARDT. 1952. Notes on the estimation of survival rates from age distributions of deer. Paper presented at 14th Midwest Wildl. Conf., Des Moines, Iowa, December 17-19.

HUNTER, G. N. 1947. Physical characteristics of

Colorado mule deer in relation to their age classes. Colo. Fish and Game Dept., 38pp.

JONES, F. L. 1953. Ageing the Inyo mule deer. Proc. Conf. West. Assoc. of State Game and Fish Comm., 33:209-219.

LEOPOLD, A. S., T. RINEY, R. MCCAIN, AND L. TEVIS, JR. 1951. The Jawbone deer herd. Calif. Div. Fish and Game, Game Bull. No. 4, 139pp.

MCLEAN, D. D. 1936. The replacement of teeth in deer as a means of age determination. Calif. Fish and Game, 22:43-44.

MORELAND, R. 1952. A technique for determining age in black-tailed deer. Proc. Conf. West. Assoc. of State Game and Fish Comm., 32:214-219.

PETERSON, R. L. 1955. North American moose. (Appendix A—A study of mandibular toothwear as an index to age of moose by R. C. Passmore, R. L. Peterson and A. T. Cringan). U. of Toronto Press, 280pp.

RINEY, T. 1951. Standard terminology for deer teeth. J. Wildl. Mgmt., 15:99-101.

ROBINETTE, W. L. AND W. JENSEN. 1950. A simplified method for determining the age of mule deer. Utah Dept. of Fish and Game, Infor. Bull. No. 1, 4pp.

SCHEFFER, V. B. 1950. Growth layers on the teeth of Pinnipedia as an indication of age. Science, 112:309-311.

SEVERINGHAUS, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. J. Wildl. Mgmt., 13:195-216.

———. 1954. Wariness as an influence on age composition of white-tailed deer killed by hunters. N.Y. Fish and Game Jour., 1:98-109.

STEVENS, C. L. 1953. Use of checking station data in determining the size of the New Hampshire deer herd. Prog. Rep., For. Dept., U. of N.H. 5pp. mimeo.

Received for publication March 9, 1956.

A SUMMER WHISTLING COCK COUNT OF BOBWHITE QUAIL AS AN INDEX TO WINTERING POPULATIONS[1]

Walter Rosene, Jr.

U.S. Fish and Wildlife Service

For many years populations of the bobwhite quail (*Colinus virginianus*) have been censused with the aid of bird dogs in late fall and winter months when these birds form into coveys. This type of count, although important in population studies, is made too late to be of value to the administrator in predicting the success of an oncoming hunting season. An early evaluation from different physiographic regions might serve to shift hunting pressure from less to more populated coverts for a more successful harvest. Therefore, biologists have been attempting to develop a technique that can be applied in the summer to predict with a fair degree of accuracy what the coming fall and winter population will be. Such a method, if practical, should aid the administrator.

Evidence from several sources indicates that whistling-cock counts in summer are useful as a basis for predicting populations for the subsequent fall. Bennitt (1951), although lacking fall and winter population data, found a close correlation between a summer whistling-cock call index and actual hunting success the following fall. From his summer data, he predicted what the hunting success would be in various "zoogeographic" regions of Missouri. A similar method has been used in Indiana (Reeves, 1951). The present study compares summer whistling-cock counts in 1950-53 with subsequent fall and winter populations on the same areas in Alabama and South Carolina. With modifications, Bennitt's technique for the summer whistling-cock count was fitted into the experimental design for this study.

Bennitt (*op. cit.*) used a roadside count, always starting at sunrise. His route con-

[1]This study is a contribution from the Patuxent Research Refuge, Laurel, Maryland, of the Branch of Wildlife Research and a part of the Service program of Wildlife Investigations on Agricultural Lands. Assistance in the statistical portion was secured from E. F. Schultz, Jr., Agricultural Experiment Station, Alabama Polytechnic Institute, Auburn, Alabama, who helped in computing the analyses of variance. Development of the regression formula and the prediction table was carried out by A. L. Finkner, Department of Experimental Statistics, North Carolina State College, Raleigh, North Carolina, who also aided greatly by critically editing the entire section on analysis of data.

sisted of "about 30 miles of road," on which "the observer stops at one-mile intervals along his route for an hour, counting the birds at each stop." He remains "at each stop until he has heard all cocks whistling 'bobwhite' within earshot; this usually takes two or three minutes."

METHODS

Preliminary observations before the present study indicated that "bobwhiting" of males seemed to reach a peak at certain intervals, then frequency of calls would decline. Therefore, in the course of counting, sufficient time was spent at each listening stop to record calls through one or more of these peak periods. Calls from individual males were distinguished sufficiently well so that they could be plotted with accuracy on aerial photos. The average time of stops, including both listening and driving time, was 11.5 minutes. Driving time between stops averaged 3.5 minutes, so that approximately 8 minutes was spent listening at each stop. At listening stations, the observer walked a few paces from the auto so that sounds would be less obstructed, taking care to avoid making unnecessary noise.

The count was made each year from June 20 to July 10, a period when nesting activities normally are most intense in the southeastern states. In preparation, routes and listening stops, with estimated audible range from each, were marked on aerial photographs of the areas. Stops were arranged so that "bobwhite" calls over all parts of each tract could be heard. During the first year, 5,458 acres were used for study; in the last three years, 12,273. Four study areas totaling 5,571 acres were located near Union Springs, Alabama, and 6 areas with 6,702 acres in South Carolina near Ridgeland, Georgetown, and Pineville. Size of study areas varied from 507 acres to 1,745.

Two successive mornings were spent on each individual area and "bobwhite" calls were plotted for each morning. After the two trips the total number of callers was estimated. A whistling cock heard on either one or both mornings from a specific location was counted as one individual.

On the first morning of the first yearly count, 1950 for some areas and 1951 for others, the time of arrival was recorded for each listening stop. Each stop was visited at about the same time and date on subsequent years. The count was started each morning at about 25 minutes after official sunrise. An average of one hour and 25 minutes was required to complete each day's count.

The amount of light falling in the immediate vicinity of each stop at the time of listening was recorded in foot lamberts. A General Electric exposure meter (type DW-58) was used, holding it in the hand with the opening at zenith. Care was exercised to avoid obstructions between meter and sky within the angle of incidence.

Bennitt (*op. cit.*) checked wind velocity, humidity, and type of road as factors causing variation in the number of calls. He found no correction necessary for these fac-

TABLE 1. — NUMBERS PER 1,000 ACRES OF WHISTLING COCKS HEARD IN SUMMER AND COVEYS FOUND IN SUBSEQUENT HUNTING SEASONS

		1950		1951		1952		1953		Average		Coveys per Whistling Cock
		Cocks	Coveys	Cocks	Coveys	Cocks	Coveys	Cocks	Coveys	Cocks	Coveys	
Alabama												
Study area	1	32.3	37.0	33.1	37.0	38.6	40.9	33.1	44.1	34.3	39.8	1.16
	2	—	—	16.2	23.9	22.9	21.6	27.6	19.5	22.2	21.7	0.98
	3	9.2	28.4	13.7	13.7	21.1	22.9	27.5	30.7	17.9	23.9	1.34
	4	—	—	18.0	18.0	23.8	15.7	25.0	22.6	22.3	18.8	0.84
Average		20.7	32.7	20.3	23.2	26.6	25.3	28.3	29.2	24.4	26.9	1.10
South Carolina												
Study area	1	—	—	25.1	24.0	26.3	18.3	18.3	20.6	23.2	21.0	0.90
	2	—	—	18.2	12.2	10.1	14.2	13.2	8.1	13.8	11.5	0.83
	3	—	—	18.1	10.7	13.2	8.3	13.2	9.1	14.8	9.3	0.63
	4	—	—	32.1	20.8	30.2	34.0	32.1	28.3	31.5	27.7	0.88
	5	20.7	29.6	22.2	34.8	25.2	20.0	15.5	22.2	20.9	26.7	1.28
	6	16.6	9.2	16.6	15.2	14.9	13.5	18.3	18.9	16.6	14.2	0.85
Average		18.7	19.4	22.1	19.6	20.0	18.1	18.4	17.9	20.0	18.6	0.93
Total average		19.7	26.1	21.3	21.0	22.6	20.9	22.4	22.4	21.8	22.0	1.01

TABLE 2. — ANALYSIS OF DATA BY INDIVIDUAL YEARS AND AREAS

Summer Whistling Cocks	Hunting Season	$\bar{X}$	$\bar{Y}$	b	β	F-values
1950	1950-51	19.7	26.1	0.60	−2.67 to 3.87	0.63
1951	1951-52	21.3	21.0	0.85	0.00 to 1.70	5.27*
1952	1952-53	22.6	20.9	1.02	0.58 to 1.48	27.61**
1953	1953-54	22.4	22.4	1.15	0.53 to 1.77	18.32**
Summary all years						
Alabama areas		24.4	26.9	0.81	0.29 to 1.33	11.38**
South Carolina areas		20.0	18.6	0.86	0.40 to 1.33	15.18**
Combined areas		21.8	22.0	0.92	0.60 to 1.24	34.09**

$\bar{X}$ = mean of whistling cocks per 1,000 acres of individual areas
$\bar{Y}$ = mean of coveys per 1,000 acres of individual areas
b = regression coefficient
β = limits of b with .95 confidence
F = reduction due to regression (mean square)/deviation from regression (mean square)
* Significant at .05 level
** Significant at .01 level

tors for records made on normal days and terrain. Observations made in the present study conformed to the "normal" limitations he established for these factors.

In Missouri, Bennitt found a relationship between call index and temperature; he therefore corrected actual indices "to bring all values to parity with those in the commonest interval, 70°-74.5° F. . ." At the peak of nesting activity in the Southeast, weather conditions are fairly stable. Temperature at sunrise usually is between 70° and 75° F. Twelve of 27 records at sunrise were within this range; 6 others were above and 9 below. Maximum morning temperature recorded on these field trips was 79°, and 66° was minimum. Due to the close proximity of these temperatures to the 70°-74.5° interval established by Bennitt, no corrections were made.

CENSUS RESULTS

During the four years of study, 901 cocks were heard whistling, and 910 coveys were found in subsequent hunting seasons. This, as well as the summary of cocks and coveys of all areas in Table 1, suggests a relationship between the two. In 1950 on Alabama study area 3, there was a greater discrepancy between whistling cocks and fall coveys than was found on any other area in any year of the study. Each year, Alabama study areas had more summer whistling cocks and winter coveys per unit of area than the South Carolina tracts, but the close relationship between numbers of cocks and coveys persisted.

The annual summary by states (Table 1) points out that when a larger number of whistling cocks was recorded in a given year than in the previous one, more coveys were also found and, correspondingly, a drop in number of calling cocks was followed by a reduced number of fall coveys. These annual up-and-down population changes in cocks and coveys appeared when data for both states were combined. A downward year-to-year trend was found on Alabama areas at the same time that an upward trend appeared in South Carolina. The combination of data indicates that annual fluctuations which were found between the cock-covey relationship were more or less localized by area. They tended to compensate one another when summarized on a regional basis.

Certain areas were more productive than others, i.e., they had more whistling cocks and also more coveys. The same local variation was true in both states. However, Alabama areas seemed to be generally more productive than those in South Carolina.

ANALYSIS OF DATA

Summaries of the regression analyses are presented in Table 2. F values testing the significance of cock-covey relationships (re-

gression of numbers of coveys on number of whistling cocks) are given by years, by location, and combined. The relationship was positive each year and removed a significant portion of the variability in coveys per 1,000 acres at the 5 per cent level for each year except the first. The lack of significance in 1950 reflects the amount of variation in the data when only four areas totaling 5,458 acres were used. In that year, only 24.2 per cent of the error could be accounted for by the regression of coveys per 1,000 acres on number of whistling cocks per 1,000 acres. Possible causes could have been that (1) the total of these areas was too small with variations between units too great, or (2) errors may have occurred because of inexperience of the listener at the start of the study.

An analysis of variance to test possible differences between yearly regression coefficients (b in Table 2) gave a value less than 1. Therefore, there is no significant difference between the coefficients. Since there is no evidence of more than a single population, the results of all years and locations are pooled to find the average regression coefficient, $b = 0.92$ and its 95 per cent confidence limits ± 0.32. In this analysis, 51 per cent of the variation in number of coveys is explained by knowledge of number of whistling cocks during the previous summer.

Estimates[1] for the last three years were made, utilizing the relationship between X and Y for the preceding years and the measure of X in the current year. These predicted values and their corresponding standard errors are shown in Table 3 along with the mean number of coveys found per 1,000 acres for that season.

TABLE 3

Hunting Season	$\bar{y}$	$\hat{\bar{y}}$	$s_{\hat{\bar{y}}}$
1951-52	21.0	27.1	±6.6
1952-53	20.9	23.7	±3.0
1953-54	22.4	22.5	±2.5

The predicted mean value is converging on the actual mean value as more information over years is available. As would be expected, the precision also increases as more years are included.

If a prediction is to be made for a specific area (i.e. an estimate of the number of whistling cocks has been made for one observational unit, and one wishes to predict the number of coveys in that area using the relationship established over the four seasons), the variance of $\hat{Y}$ (any predicted Y) is the sum of two independent variances: the variance of the mean ($\bar{y}$) and the variance of the regression coefficient (b). The standard error of a point on the regression line is

$\pm\sqrt{1.3806 + .025x^2}$ where x = deviation from the mean.

Values of X were selected at the extremities of the regression line and near the mean ($\bar{x}$, $\bar{y}$) for determining the shape of the curves CD and EF shown in Fig. 1.

As indicated in Fig. 1, any error in the slope of $\hat{Y}$ becomes more pronounced as one considers points more distant from the center of the distribution, so any attempt to predict coveys from whistling cocks becomes more hazardous toward either extremity of $\hat{Y}$, from $\bar{x}$ $\bar{y}$.

DISCUSSION

Various viewpoints have been advanced as to what a whistling cock represents. Many ornithologists contend that he is the mate of a brooding female. Bennitt (*op. cit.*) says that a few mated cocks call "bobwhite." After much field work, Stoddard (1932) is positive that "... the 'bobwhite'

[1]The predictions desired here do not fit standard regression theory and are made as follows:

$$\hat{\bar{y}} = \bar{y}_m + b\,(\bar{x}_k - \bar{x}_m)$$

where

- $\bar{x}_k$ = mean number of whistling cocks per 1,000 acres counted in year t,
- $\bar{x}_m$ = mean number of whistling cocks per 1,000 acres over (t-1) years,
- $\bar{y}_m$ = mean number of coveys found per 1,000 acres over (t-1) years, and
- b = regression coefficient for Y on X over (t-1) years.

The variance of the predicted mean value is

$$s^2_{\hat{\bar{y}}} = s^2_{y \cdot x}\left[\frac{1}{n} + \frac{(\bar{x}_k - \bar{x}_m)^2}{\Sigma x^2}\right] + \frac{b^2 s^2_x}{k}$$

where

- $s^2_{y \cdot x}$ = the squared standard error of estimate over (t-1) years,
- n = the number of observations over (t-1) years,
- Σx^2 = sum of squares of X over (t-1) years,
- s^2_x = variance for whistling cocks in year t on an individual observation basis, and
- k = number of observations in year t.

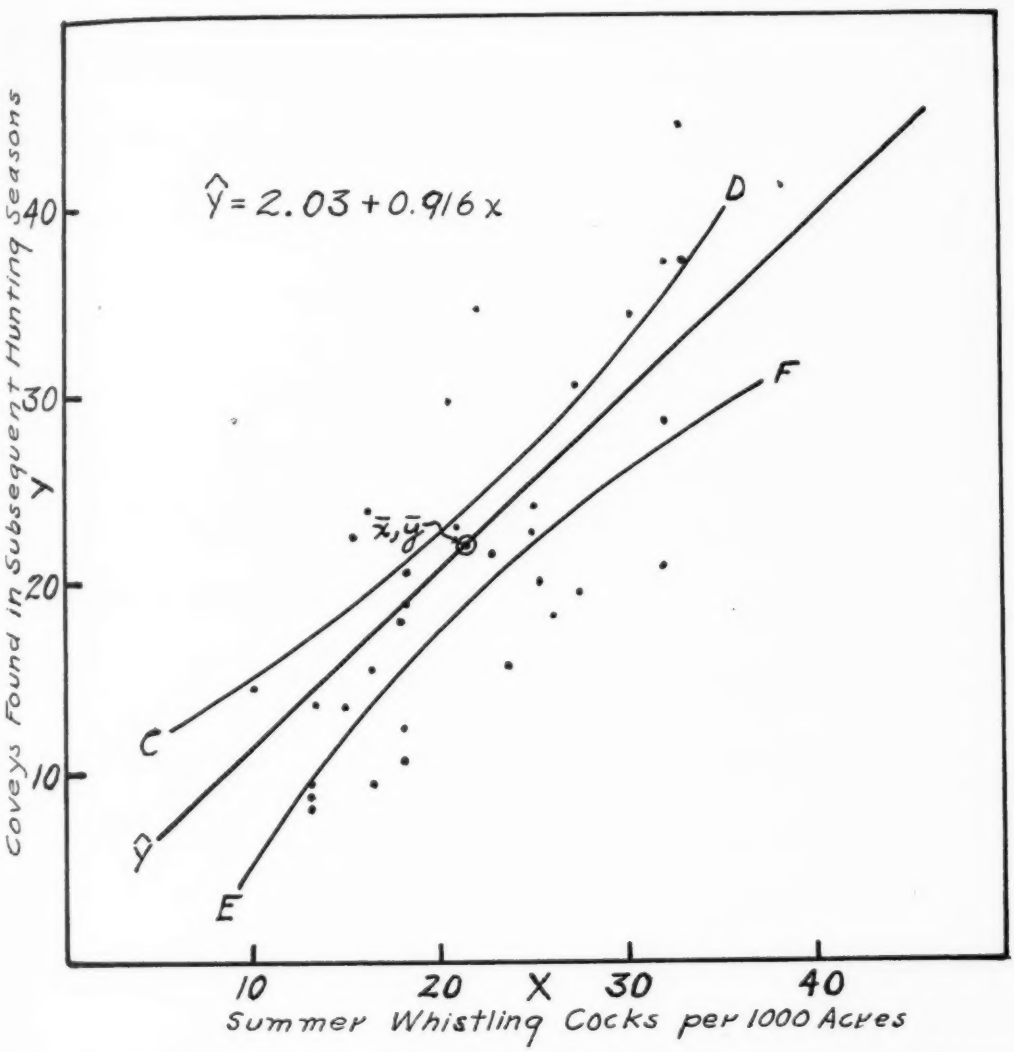


FIG. 1. The relationship between the number of whistling cock quail heard in summer and quail coveys found in subsequent hunting seasons.

call is largely a call for a mate, and that the whistling so commonly heard during the summer months may be largely attributed to unmated cocks." In application, he states that "the number of persistently whistling cock quail in early summer furnishes a key to the breeding population where the sex ratio is known, since such calling is largely from unmated, or surplus cocks." Bennitt was satisfied with "the truth of Stoddard's statement: that the number of whistlers just about fits the known surplus of cocks." Stoddard concluded that "the method is of no value except in the early part of the nesting season when 'bobwhite' whistling is general. At this time it will give an approximation of the breeding population."

Recent techniques (Petrides and Nestler, 1943) for age determination show that half of the young quail usually have hatched by July 10, with the peak of the nesting activity usually between June 20 and July 10. The majority of "bobwhite" calling activity also occurs at this time. Therefore, most mating would have to occur several weeks prior to the peak of hatching and before "bobwhite"

calling reaches its peak. As conclusions of several studies vary, more research is in order to determine the relationship of a whistling cock to the composite summer quail population.

Areas used in this study had both high and low populations. The fact that certain areas always had a relatively large number of whistling cocks and a correspondingly high winter population indicates the value of a management program that includes practices effective in each season. Such was true for area 1 in Alabama.

Area 3 in South Carolina had poor quail habitat in both summer and winter. As a result, a low number of whistling cocks was found despite the fact that adequate brood stock had remained at the end of the hunting season. Undesirable nesting conditions resulted in the smallest number of coveys per 1,000 acres of any area under study. Coveys per whistling cock were also lowest.

Area 3 in Alabama had a high percentage of the area in woodland. This is not conducive to nesting. However, coveys per whistling cock were higher than on any other tract due to a burning and timber-management program that produced the greatest number of coveys from the breeding population.

Areas with an average quail-producing potential (Alabama 2 and 4 and South Carolina 1) had average numbers of whistling cocks. The breeding population may produce higher or lower corresponding numbers of coveys depending on (1) the effectiveness of the management practices that encourage quail to bring off successful broods and (2) the quality and abundance of food and cover necessary to retain young and adults in the vicinity of the nest throughout the fall and winter. Weather may also be a factor.

Minimum-size area was set at 500 acres. The maximum acreage that one investigator can cover in the early morning while calling activity is most intense is approximately 1,700. Data from this study demonstrated that by using many areas within these limits, with a total of at least 12,000 acres all within a similar environment, a trend in the subsequent winter population could be predicted. A larger acreage would give more accuracy.

SUMMARY AND CONCLUSIONS

A summer whistling-cock count of bobwhite quail was made and compared with covey numbers in subsequent hunting seasons in 1950-53 on 4 areas in Alabama and 6 in South Carolina. Findings involved a total of 901 whistling cocks and 910 coveys. Study area acreage in Alabama was 5,571 and 6,679 in South Carolina.

There was a relationship between the numbers of whistling cocks heard in summer and coveys found in subsequent hunting seasons when the data were summarized annually and by states.

An increase or decrease in the number of whistling cocks heard in summer over the previous year was followed by an increase or decrease respectively in coveys in the subsequent hunting season when the results were summarized by states.

Using this technique, it is possible to predict by physiographic types the number of coveys that will be found in winter from the number of whistling cocks heard the previous summer, if areas 500-1,700 acres in size are used with a total of at least 12,000 acres. The confidence limits of the prediction increase both below and above the mean.

LITERATURE CITED

BENNITT, R. 1951. Some aspects of Missouri quail and quail hunting. Mo. Cons. Comm., Tech. Bull. No. 2, 51pp.

PETRIDES, G. A. and R. B. Nestler. 1943. Age determination in juvenile bob-white quail. Amer. Mid. Nat., 30:774-782.

REEVES, M. C. 1951. Whistling quail count. Outdoor Indiana, 18(10):10,19.

STODDARD, H. L. 1932. The bobwhite quail, its habits, preservation and increase. Charles Scribner's Sons, N.Y. 559pp.

Received for publication September 10, 1956.

RANGE USE, FOOD HABITS, AND AGRICULTURAL RELATIONSHIPS OF THE MULE DEER, BRIDGER MOUNTAINS, MONTANA[1]

Bruce T. Wilkins

Montana Fish and Game Department, Stanford, Montana

A pronounced increase in Rocky Mountain mule deer (*Odocoileus h. hemionus*) numbers has occurred in recent years in the Bridger Mountains, Gallatin County, Montana. Residents report that, as late as 1948, deer were quite scarce and not frequently seen. Today deer are commonly seen, and a large population is evidenced by overused browse plants as well as by damage to agricultural products. Predator control, buck-only seasons (until 1952), and a scarcity of hunters due to the precipitousness of the terrain have undoubtedly been contributing factors to this increase.

Except for casual observations, no attempt had been made to secure basic ecological information necessary for proper management of this herd. Specific information on food habits and range use was lacking, not only for this area but for much of the state. To help clarify the intricate problems associated with the management of this game animal, a study was carried out on a full-time basis during the summer and winter months, and periodically in the fall and spring, from June 16, 1955, to May 7, 1956. Food habits, range use, and agricultural relationships were emphasized. Although the study was conducted primarily to aid in the future management of the mule deer in the Bridger Mountains, it was felt that the results would have definite application to the management of this animal in similar situations throughout the state.

Appreciation for aid during the study is extended to the following: Don C. Quimby for technical supervision and guidance in writing the manuscript; Joseph Townsend, District Game Biologist, for direction and assistance in the field; J. C. Wright and

[1]A joint contribution from Montana State College, Agricultural Experiment Station, Project No. MS 844, Paper No. 389, Journal Series, and the Wildlife Restoration Division, Project W-73-R-1, Montana Fish and Game Department.

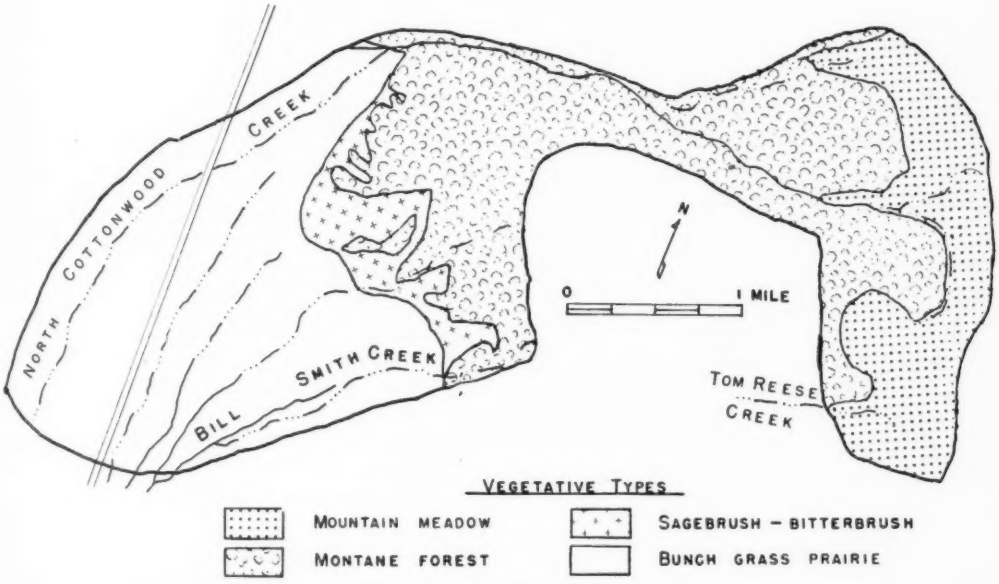


FIG. 1. Map of the study area.

FIG. 2. Vegetative types at high elevations: foreground, mountain meadow; right rear, upper montane forest; left rear, steep mountain peaks.

W. E. Booth for aid in identifying plant materials. Further thanks are extended to the ranchers in the area, and particularly to Mr. and Mrs. Ralph Armstrong for their close cooperation. During the course of the study the author was employed by the Montana Fish and Game Department under Federal Aid Project W-73-R-1.

DESCRIPTION OF THE AREA

The Bridger Mountains are situated in southwestern Montana, north and east of Bozeman. Their west slope is composed primarily of shale and limestone formations. The mountains are quite steep at their base (elevation 5,600 feet) and at their peaks (maximum elevation 9,669 feet). The numerous canyons generally extend in an east-west direction. That part of the range involved in the food-habits study was restricted to 6.5 square miles on the western slope (Fig. 1). This area was vegetatively typical of that part of the slope where the foothills area is devoted to agriculture.

Four distinct vegetative types were recognized on the study area. Scientific and common names of plants follow those of Booth (1950) and Wright and Booth (1956). In cases where these authors did not cite common names, those given by the American Joint Committee on Horticultural Nomenclature (1942) are used.

Mountain meadow.—This type occurs at the base of the steep peaks (Fig. 2). The vegetation is characterized by grass and grass-like plants. Purple oniongrass (*Melica spectabilis*), Idaho fescue (*Festuca idahoensis*), and sedges (*Carex* spp.) are the principal species. The remainder of the vegetation is composed of various forbs with some intermittent patches of Douglas-fir (*Pseudotsuga taxifolia*) and alpine fir (*Abies lasiocarpa*). This mountain-meadow type occurs from 8,600 to 7,800 feet, extending farther downward in the creek bottoms. The high altitude together with abundant springs keeps this part of the area moist and the

FIG. 3. Vegetative types at lower elevations: foreground, bunchgrass prairie; midsection, sagebrush-bitterbrush; rear, lower montane forest.

vegetation succulent approximately a month after the vegetation at the base of the mountain has dried up.

Montane forest.—This type is characterized by a Douglas-fir forest (Figs. 2 and 3) that has not been logged commercially since approximately 1900. The understory is composed primarily of browse species and elk sedge (*Carex geyeri*). The principal browse species are common juniper (*Juniperus communis*) and common snowberry (*Symphoricarpos albus*). This type occurs from 8,600 to 6,000 feet. It extends downward in elevation another 200 feet on the north-facing exposures (Fig. 3).

Sagebrush-bitterbrush.—This type occurs on the steep mountain base from approximately 6,400 to 5,600 feet (Fig. 3). Big sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and Rocky Mountain juniper (*Juniperus scopulorum*) are the characteristic plants. Grasses are next in abundance with cheatgrass (*Bromus tectorum*) and bluebunch wheatgrass (*Agrypyron spicatum*) predominant. Balsamroot (*Balsamorhiza sagittata*) and field chickweed (*Cerastium arvense*) appear to be the most common forbs.

Bunchgrass prairie.—This type is located on the alluvial fan at the base of the mountain (below 5,600 feet) and is used extensively for agricultural purposes (Fig. 3). The untilled portion is grazed. Here the principal grasses are Idaho fescue, bluebunch wheatgrass, and needle-and-thread (*Stipa comata*). Balsamroot, yarrow (*Achillea lanulosa*), and arnica (*Arnica* spp.) are abundant forbs. Some big sagebrush also occurs on this type. In the more moist situations other woody plants occur, the most common species being black poplar (*Populus trichocarpa*) and black hawthorn (*Crataegus douglasii*). That portion that is tilled is devoted primarily to growing wheat, or alfalfa and smooth brome (*Bromus inermis*) hay.

USE OF VEGETATIVE TYPES

Deer use of vegetative types was determined by morning and evening observations with a 7 × 35 binocular and a 20-power spotting scope. Approximately 3,500 observations of deer were recorded during the study. Observations were made on the bunchgrass prairie and sagebrush-bitterbrush types throughout the study and from July 15 to September 12 on the mountain-meadow type. One aerial flight over the entire study area was made on November 25.

Sagebrush-bitterbrush was the most heavily utilized type. From June 16 to August 14, the average number of deer per observation (41 observations) seen there was five. The number of young fawns observed (including four that were caught and tagged) suggest that parturition occurs either on this type or on the lower montane forest in this region. From August 15 to October 31, the number of deer per observation dropped to slightly under two for 25 observations. This was probably related to the arid conditions present at this lower elevation during that time. On November 7, when 45 deer were observed, and throughout the remainder of the study, large numbers of deer were present here. Based on 71 observations from November 7 to March 19, this concentration averaged about 25 per observation. Over 90 per cent of these deer were observed on south-facing exposures. These slopes seldom remained snow-covered for periods exceeding one or two days, and provided the principal wintering areas for the herd. The slopes not receiving the direct rays of the sun remained snow-covered throughout the winter. Use of the sagebrush-bitterbrush type continued through the remainder of the study, the number of deer averaging 46 for 11 observations. This increase over the average number seen in the November to March 19 observations is believed to have been due to the earlier and later times of day at which observations were carried out.

The bunchgrass prairie was moderately used from June 16 to October 31 (an average of 4 deer per observation for 90 observations). From August to October most of these deer were in close proximity to Cottonwood Creek or Bill Smith Creek, the two main creeks in the area. From December through March 19 this type was continuously covered by one to two feet of snow, and few deer were seen (less than one deer per observation for 75 observations). Deer at haystacks were not considered in these counts. By March 20 much of this area was clear of snow, and on that date 18 deer were seen feeding on this type. From that date until the conclusion of the study (May 7) there was an increase in use, indicated by an average of 13 deer per observation for 13 observations.

In the montane forest, trees restricted vision so that few observations were carried out there. The absence of deer from other areas during most days made it apparent that this area was used for shelter and rest. The lower portion was used as escape cover for the deer on the sagebrush-bitterbrush type and the upper portion was visited by deer using the mountain meadows. No tracks or deer were seen in the upper half of this type on a flight that I made on November 25, but deer and tracks were present on the lower half.

Deer used the mountain meadows extensively in the summer. This is indicated by an average of 11 deer seen in the 23 observations made there. The only other observation on this type was in the course of the November 25 flight, when no deer or tracks were seen.

FOOD HABITS

The techniques used to determine food habits were similar to those used by Saunders (1955) and Cole (1956) and consisted of rumen analysis together with the recording of feeding observations. Where deer were seen to feed, feeding observations were made by examining areas for signs of recent plant use. Direct observation of use was recorded when possible. During the winter it was possible to follow deer tracks and determine use of certain plants.

Twenty-seven deer were collected from June 22, 1955, to May 6, 1956, and a one-quart rumen sample was obtained from each. A minimum of two deer per month was obtained with the exception of May and June. Only one deer was taken in each of these months. Three were collected in both October and January. Five were obtained in December. Collections were generally made at approximately 15-day intervals. The

rumen samples were preserved in a 10 per cent formalin solution. In the laboratory, the sample was washed with water on consecutive 3-mm. and 2-mm. screens. The material retained on the 3-mm. screen was then placed in a pan of water, and the identifiable portions removed. Identification as to species, genus, family, or general group was then made by comparison with a reference plant collection After drying on paper toweling to remove excess moisture, the volumes (to the nearest 0.5 per cent) of the segregated portions were determined by water displacement. The same material was then air-dried and weighed to the nearest 0.01 gram. Material with a volume less than 0.5 cc. was recorded as "trace." The unidentifiable material on the 3-mm. screen was included with that on the 2-mm. screen. Volume and weight were taken. A total of 4,403 cc. of material from the 27 rumen samples was obtained, of which 32 per cent was identified. The percentage of the stomach contents that any one item constituted for a season or other period was computed by the aggregate percentage method (Martin, *et al.*, 1946). This involved a determination of the percentage of the total identifiable material in each rumen sample that the item in question constituted. The percentages for all stomachs for any period were then averaged (Table 1).

Summer (June, July, August, to mid-September)

Six rumen samples were included in this season (1 June, 2 July, 2 August, and 1 early September). Three were from deer collected on the mountain meadow, one was from a deer on an alfalfa field, and two were from deer on the sagebrush-bitterbrush type. One of the latter had been seen to feed earlier on the bunchgrass prairie. Forbs (12 items) constituted 77 per cent by volume and 74 per cent by weight of the samples. Salsify (*Tragopogon dubius*) and alfalfa were important identifiable forbs. Other important identifiable forbs included balsamroot, fewflower aster (*Aster modestus*), common dandelion (*Taraxacum officinali*), and silvery lupine (*Lupinus argentea*). Unidentified forbs made up 22 per cent by volume and 22 per cent by weight. Browse (3 species) formed 19 per cent of the samples by volume and 21 per cent by weight, with bitterbrush and thin-leaved huckleberry (*Vaccinium membranaceum*) being the important browse species. Grass composed 3 per cent of the volume and 4 per cent of the weight.

Undue importance was probably given to alfalfa and bitterbrush by the limited sampling. The one sample from the deer taken on an alfalfa field contained 71 per cent alfalfa by volume and 78 per cent by weight. The only other occurrence of alfalfa (2 per cent by volume and 2 per cent by weight) involved the specimen taken on June 22. In the one sample from a deer seen only on the sagebrush-bitterbrush type, bitterbrush composed 87 per cent by volume and 89 per cent by weight.

The most important browse species in the samples from deer taken on the mountain meadow was thin-leaved huckleberry. This species was present in all the samples from this type, and only in these samples. Most of the unidentified forbs came from deer collected on the mountain meadow.

Three hundred and twelve feeding observations were made during this season. The breakdown by types was: mountain meadow 162; sagebrush-bitterbrush 26; bunchgrass prairie 124 (including 70 from alfalfa fields). Forbs constituted 74 per cent of the observed plant use. Alfalfa and balsamroot were the most important species. Browse (20 per cent) was second in importance, with bitterbrush being the major species. Grass formed 2 per cent of the observed plant use.

Fall (mid-September, October, November)

Six rumen samples were analyzed (1 late September, 3 October, and 2 November). The September and October 8 samples were from deer collected on the bunchgrass prairie near Cottonwood Creek. The remaining four samples were collected from deer on the sagebrush-bitterbrush type. Browse was most important in this season (73 per cent by volume, 75 per cent by weight). Bitterbrush and western snowberry (*Symphoricarpos occidentalis*) were the most important of the 9 browse species. Forbs (4 items) constituted 24 per cent by volume and 22 per cent by weight. Alfalfa and balsamroot were the more important members of this group. Grass composed 3 per cent by volume and 3 per cent by weight.

TABLE 1. — MULE DEER FOOD HABITS AS DETERMINED BY ANALYSIS OF 27 RUMEN SAMPLES AND 505 INSTANCES OF PLANT USE
(T = trace—less than 0.5 per cent)

	Summer				Fall		Winter				Spring	
	Obs. Instances of Use		Six Rumen Samples		Six Rumen Samples		Obs. Instances of Use		Eleven Rumen Samples		Four Rumen Samples	
Plants[1]	%	No.	% Vol.	% Wt.	% Vol.	% Wt.	%	No.	% Vol.	% Wt.	% Vol.	% Wt.
Purshia tridentata	9	29	15	16	41	44	11	22	14	18	2	2
Artemisia tridentata	1	2	—	—	6	5	17	33	25	24	16	18
Juniperus scopulorum	1	2	—	—	T	T	16	31	13	17	5	8
Rosa engelmani	2	5	1	1	2	2	—	—	3	3	T	T
Prunus virginiana	2	5	T	T	4	3	9	18	1	2	1	1
Populus trichocarpa	1	2	T	T	3	3	2	3	T	T	—	—
Symphoricarpos occidentalis	—	—	—	—	11	11	—	—	1	1	—	—
Pyrus spp.	—	—	—	—	1	1	—	—	5	3	—	—
Ribes setosum	1	4	—	—	3	3	—	—	—	—	—	—
Crataegus douglasii	T	1	—	—	2	3	—	—	—	—	—	—
Philadelphus lewesi	—	—	T	T	—	—	2	4	2	2	—	—
Pseudotsuga taxifolia	—	—	—	—	T	T	1	1	2	2	—	—
Alnus sinuata	2	5	—	—	—	—	—	—	T	T	—	—
Vaccinium membranaceum	—	—	3	4	—	—	—	—	—	—	—	—
Rubus spp.	1	2	—	—	—	—	—	—	—	—	—	—
Unidentified browse	—	—	—	—	—	—	—	—	T	T	—	—
Browse totals	20	57	19	21	73	75	58	112	66	72	24	29
Balsamorhiza sagittata	11	34	9	8	9	8	18	34	12	11	10	10
Medicago sativa	17	52	12	13	11	12	—	—	T	T	12	12
Lupinus argentea	2	7	4	4	T	T	—	—	1	1	1	1
Cerastium arvense	—	—	T	T	T	T	3	5	4	3	2	1
Achillea lanulosa	—	—	T	T	T	T	2	3	1	1	2	2
Gaillardia aristata	1	3	T	T	T	T	—	—	T	T	—	—
Phacelia leucophylla	—	—	T	T	—	—	1	1	T	T	—	—
Descurainia pinnata	T	1	—	—	T	T	—	—	T	T	—	—
Artemisia ludoviciana	—	—	—	—	T	T	3	6	T	T	—	—
Lactuca scariola	3	8	3	2	—	—	—	—	T	T	—	—
Geranium viscosissimum	—	—	1	2	—	—	—	—	—	—	1	1
Antennaria microphylla	—	—	—	—	1	1	—	—	—	—	1	1
Tragopogon dubius	T	1	12	10	—	—	—	—	—	—	—	—
Aster modestus	—	—	5	5	—	—	—	—	—	—	—	—
Taraxacum officinale	1	3	4	3	—	—	—	—	—	—	—	—
Delphinium occidentale	—	—	3	3	—	—	—	—	—	—	—	—
Heracleum lanatum	T	1	1	1	—	—	—	—	—	—	—	—
Thalictrum sparsiflorum	—	—	1	1	—	—	—	—	—	—	—	—
Valeriana occidentalis	T	1	T	T	—	—	—	—	—	—	—	—
Haplopappus acaulis	7	21	—	—	—	—	—	—	—	—	—	—
Crepis spp.	5	15	—	—	—	—	—	—	—	—	—	—
Agoseris glauca	4	12	—	—	—	—	—	—	—	—	—	—
Townsendia parryi	4	12	—	—	—	—	—	—	—	—	—	—
Erigeron glabellus	3	10	—	—	—	—	—	—	—	—	—	—
Castilleja miniata	3	8	—	—	—	—	—	—	—	—	—	—
Iris missouriensis	2	6	—	—	—	—	—	—	—	—	—	—
Parnassia fimbriata	2	5	—	—	—	—	—	—	—	—	—	—
Astragalus drummondi	1	2	—	—	—	—	—	—	—	—	—	—
Angelica arguta	T	1	T	T	—	—	—	—	—	—	—	—
Artemisia canadensis	—	—	—	—	—	—	4	7	—	—	—	—
Claytonia lanceolata	—	—	—	—	—	—	—	—	—	—	4	3
Ranunculus glaberrimus	—	—	—	—	—	—	—	—	—	—	3	2

(Continued on next page)

TABLE 1. — Continued

Plants[1]	Summer				Fall		Winter				Spring	
	Obs. Instances of Use		Six Rumen Samples		Six Rumen Samples		Obs. Instances of Use		Eleven Rumen Samples		Four Rumen Samples	
	%	No.	% Vol.	% Wt.	% Vol.	% Wt.	%	No.	% Vol.	% Wt.	% Vol.	% Wt.
Fritillaria pudica	—	—	—	—	—	—	—	—	—	—	1	1
Delphinium bicolor	—	—	—	—	—	—	—	—	—	—	1	1
Veronica americana	—	—	—	—	—	—	—	—	—	—	1	1
Erigeron pumilus	—	—	—	—	—	—	—	—	—	—	1	1
Unidentified forbs	8	26	22	22	3	1	1	2	T	T	T	T
Forb totals	74	229	77	74	24	22	32	58	18	16	40	37
Gramineae	2	5	3	4	3	3	12	23	14	10	37	38
Juncus regelii	6	20	—	—	—	—	—	—	—	—	—	—
Equisetum laevigatum	T	1	—	—	—	—	—	—	—	—	—	—

[1]Twenty-one plant items that did not exceed 0.5 per cent in any one season are omitted from this tabulation: *Berberis repens, Artemisia frigida, Rhamnus alnifolia, Salix bebbiana, Acer glabrum, Penstemon albertinus, Hieracium albertinum,* Aster spp., Leguminosae, *Rudbeckia laciniata,* Liliaceae, *Smilacine stellata, Galium boreale, Capsella bursapastoris, Chenopodium album, Cirsium undulatum, Chrysopsis villosa, Heuchera ovalifolia, Arabis nuttalli, Potentilla gracilis* and *Carex geyeri.*

For the four samples from deer on the sagebrush-bitterbrush type, bitterbrush constituted over 53 per cent by volume and 58 per cent by weight for each sample. Big sagebrush was first present in the October 16 sample as a trace. In the October 23 sample it was 1 per cent by volume and 1 per cent by weight. In the November 7 and 21 samples it was, respectively: 3 per cent by volume and 3 per cent by weight; 32 per cent by volume and 28 per cent by weight.

Of the two samples from deer on the bunchgrass prairie, western snowberry averaged 33 per cent by volume and 33 per cent by weight, making it the most important species. Alfalfa was the most common forb in these two samples, constituting 16 per cent by volume and 22 per cent by weight.

Alfalfa was present in all samples for this season except the one from November 21. Alfalfa seeds found in the October 8 and 16 samples were well developed. As this forb is usually cut before seeds mature, much of this was probably taken directly from alfalfa fields rather than from haystacks.

Winter (December, January, February, to mid-March)

Eleven rumen samples (5 December, 3 January, 2 February, and 1 early March) were analyzed. All were collected from deer on the sagebrush-bitterbrush type. Nine browse items constituted 66 per cent by volume and 72 per cent by weight of the samples. Big sagebrush, bitterbrush, and Rocky Mountain juniper were important browse species. Four forbs made up 18 per cent by volume and 16 per cent by weight. The major forb was balsamroot. Grass represented 14 per cent by volume and 10 per cent by weight.

Big sagebrush ranked first in December, January, and February, and was third in the March sample with volumes and weights for respective months approximating 25 per cent. In no month did bitterbrush form over 18 per cent by volume and 21 per cent by weight of the samples. In the March sample it was 6 per cent by volume and 5 per cent by weight. An increase in the percentage of juniper and Douglas-fir in the samples from December to February was noted. Juniper volumes and weights for the respective months were: 10 per cent, 12 per cent, 13 per cent, 19 per cent, 13 per cent, 16 per cent. In December Douglas-fir was present only as "trace." In January and February it was, respectively: 1 per cent by volume, 1 per cent by weight; 7 per cent by volume and 9 per cent by weight. In the March sample juniper was the most important species (29 per cent by volume, 37 per cent by weight). No Douglas-fir was present in the March sample. Grass was present in all but one sample (January 20). It constituted 44 per cent by volume and 27 per cent by weight of the January 2 sample. In the March sample it was 28 per cent by volume and 25 per cent by weight.

Deer use of 193 plants was noted, 158 on the sagebrush-bitterbrush type and 35 on

the bunchgrass prairie. Browse constituted 58 per cent of the use noted. Big sagebrush, bitterbrush, and Rocky Mountain juniper were important. Forbs composed 32 per cent of the observations with balsamroot being the most important species. Grass use comprised 12 per cent of the observations.

Spring (mid-March, April, May)

Four rumen samples were included in this season (1 late March, 2 April, and 1 May). Three samples were from deer feeding on the sagebrush-bitterbrush type, the other from a deer on the bunchgrass prairie.

Forbs (13 species) constituted 40 per cent by volume and 37 per cent by weight. Balsamroot and alfalfa were again the major forbs. Western spring-beauty (*Claytonia lanceolata*) and sagebrush buttercup (*Ranunculus glaberrimus*) were other important forbs. Grass was equal to forbs in importance, constituting 37 per cent by volume and 38 per cent by weight. Browse was of lesser importance, composing 24 per cent by volume and 29 per cent by weight. Sagebrush and juniper were important browse species. Bitterbrush was of minor importance. In the May 6 sample sagebrush dropped to 1 per cent by volume and 1 per cent by weight, the lowest since the October 16 sample. In the two samples obtained after April 4, juniper and bitterbrush were absent, or present only as a trace. Alfalfa was present in only one sample (May 6) and composed 47 per cent by volume and 49 per cent by weight. The deer from which this sample was obtained was feeding on the sagebrush-bitterbrush type within 500 yards of an alfalfa field. The alfalfa appeared to be new growth.

Yearlong Trends and Discussion

The food-habits data indicate certain trends in the diet of the deer on the study area. During the summer forbs were most important. Browse was of less importance, and grass was little utilized. In the fall, browse became the important group and the percentage of forbs was reduced. Grass remained a minor food. Bitterbrush was the most important browse species in the fall, composing the majority of all samples from deer on the sagebrush-bitterbrush type. In the winter there was a decided decline in the use of this species, although browse remained the important group. Concurrent with the decrease in bitterbrush was an increase in the utilization of big sagebrush. Rocky Mountain juniper and Douglas-fir tended to increase in percentage as the winter progressed. Forbs were of limited importance during this period with balsamroot the most abundant forb in the samples. More grass was present in winter samples than in those for either the fall or summer, but this group was still least utilized. Going into spring, the samples indicate a shift toward grass. During the spring, forbs and grass were of equal importance. Browse was of lesser importance in this season, with big sagebrush being moderately utilized until May. Bitterbrush use steadily declined.

These seasonal trends are similar to those found by Smith (1952) in Utah. Studies by the Interstate Deer Herd Committee (1951) and Lassen, *et al.*, (1952) have also indicated a decided decline in bitterbrush consumption from fall to winter, accompanied by increased use of big sagebrush. These authors suggest that this subrogation may be in part due to a decrease in palatability or nutritional value of bitterbrush. Bissell, *et al.*, (1955) tested digestibility of bitterbrush and big sagebrush. They concluded that in periods of greatest use (November and December in their study) bitterbrush digestibility appeared to be slightly lower than in March. They further found that bitterbrush would maintain deer for several weeks with only a slight loss of weight and that it appeared to be an extremely palatable food. Big sagebrush proved to be extremely unpalatable. Smith and Hubbard (1954), testing palatability of these species in December and March, rated bitterbrush as preferred over big sagebrush. It would seem from these works that the decline in bitterbrush consumption might be best attributed to decreased availability of this browse.

In the California studies where this decreased consumption of bitterbrush was noted, the use of this plant appears to have been excessive. Such was the case on this study area, where hedging and death of plants were apparent. On May 7, 43 bitterbrush twigs, which had been marked at the base of the new growth on November 25, were remeasured. The late date for initial marking was chosen to preclude any live-

stock use. These marked twigs indicated consumption of 61 per cent of the new growth. It is estimated that about 40 per cent of the twig growth should remain on bitterbrush plants each season to maintain plant vigor and to insure adequate seed production (Hormay, 1943). Twenty-four marked twigs were not relocated, and it is felt most of these received 80-90 per cent use, resulting in the loss of markers. The part of the area on which the tagged plants were located did not receive the heaviest use by deer during the winter. As the amount of bitterbrush present in rumen samples decreased in all samples analyzed after the date on which the plants were tagged, probably the period of greatest bitterbrush use was not included in the results. All these factors would tend to give an underestimate of the percentage consumed.

Norris (1943) has indicated the possibility of undue weight being given to browse species by stomach analysis. There seems to be little question, however, that stomach analysis can be used as an indication of use, especially as related to major items in the diet. The similarity between the observed feeding percentages and the rumen analysis percentages strengthens this contention.

AGRICULTURAL DEPREDATION

Deer damage to agricultural products has been reported frequently in various sections of the country (Doman and Rasmussen, 1944; Leopold, *et al.*, 1947; Thomas and Pasto, 1955). Since 1949, numerous complaints have been made of deer damaging alfalfa haystacks and growing alfalfa in the vicinity of the study area. Three alfalfa fields and a total of 11 haystacks were under observation during this study. Two alfalfa fields in close proximity to moist areas received heavier deer use during the summer with slightly less than 2 deer for 93 observations as opposed to 0.3 deer in 61 observations on the remaining field.

Considerable damage to haystacks occurred, with as many as 50 deer observed at a stack at one time. Stacks of baled hay did not escape deer damage, but paneling with wooden panels did prevent all but minor damage. The distance from the mountain apparently had some effect on the time depredation began, with those stacks closest to the mountain receiving earliest usage. A late hunting season seemingly brought cessation of deer damage only to the one stack farthest from the mountain (approximately three-quarters of a mile away).

It is known that alfalfa hay will be eaten by deer when their natural diet is not adequate. Deer depredation on haystacks is believed to have been caused primarily by a lack of adequate amounts of palatable browse species following the restriction of the winter range by snow. Moderate damage began in November when deer first arrived en masse on the winter range. There was some snow on the hills, but the snow cover was sporadic until early December. From early December to late March all the north-facing slopes were continuously snow covered. Severe damage to the most heavily depredated stacks commenced in early December. March 20 followed three days of generally clear, mild (45° F.) weather and was the date the last extensive damage to stacks occurred. After that, the range remained free of deep snow. A few deer were later reported at the haystacks but apparently caused little damage.

HUNTING SEASONS

Since the mid-1930's, deer seasons for the general locality including the study area have been held from October 15 to November 15. From 1931 until 1952, hunting was on a "buck only" basis. Since 1951, does could also be shot at some time during the season. Postseason hunts (special open seasons after the regular hunting season) were carried out in January, 1954 and from December 20, 1955, to January 15, 1956.

Kills during the study period were estimated from checking-station data, personal contact with hunters, questionnaires, and rancher interviews. A checking station on the main road leading from the study area was operated for two days during the 1955-56 postseason hunt. Forty-two hunters were questioned as to the general area hunted, success, and whether they had had an opportunity to kill a deer. The latter was asked to eliminate the effect of poor shooting and of hunting only bucks.

Of the hunters contacted at the checking station, 45 per cent were successful, while 52 per cent had an opportunity to kill a deer.

Those who had hunted off of the road had a 66 per cent success, 93 per cent having had an opportunity to kill a deer. Thirteen (almost one-third) of the hunters never left the road; none of these had an opportunity to kill a deer. The reluctance of hunters to leave the road poses a definite problem in attempting to manage the deer in this area.

On the study area an estimated 100 deer were killed during the hunting seasons. Fourteen other deer were collected specifically for rumen analysis prior to February 17 (when the first starvation loss was noted), making a total kill of 114 up to that time. The starvation losses (all fawns); excessive use of a key plant (bitterbrush); large amounts of an emergency food, juniper (Leopold 1933), in late-winter rumen samples; and extensive haystack damage, all point to an overbrowsed winter range. That overbrowsing has not been restricted to this one year is attested by high-lined juniper, dead and hedged bitterbrush plants, and rancher reports of excessive winter deer losses (apparently starvation) and haystack damage in recent years. A need for an increased harvest is apparent.

Not until the fourth week of the season were large numbers of deer relatively accessible to hunters. Most hunters were observed to be reluctant to climb high into the mountains early in the season, or to wait until late in the season to get a deer. Rogers (1953) has indicated that most deer in Colorado are killed in the first week of a season.

SUMMARY

The range use, food habits, and agricultural relationships of the Rocky Mountain mule deer (*Odocoileus h. hemionus*) were investigated from June 16, 1955, to May 7, 1956, on a 6.5-square-mile section of the Bridger Mountains, Montana. Four vegetative types—mountain meadow, montane forest, sagebrush-bitterbrush, and bunchgrass prairie—were recognized and described. Use of vegetative types throughout the study period was determined by observations. Intraseasonal and interseasonal differences in use of vegetative types were indicated.

Food habits were determined by rumen analysis, direct observations of feeding deer, and examination of specific areas for evidence of plant use by deer. During the summer, forbs were the most important group, followed by browse and grass. The data from the fall indicate a reversal in importance of browse and forbs. During the winter, the relative positions of the groups were retained. Big sagebrush replaced bitterbrush as the most abundant species. The subrogation of bitterbrush by big sagebrush from fall to winter was apparently due to decreased availability of the former. In the spring, forbs and grass were of equal importance. Browse was the least abundant group in these samples.

The number of deer utilizing alfalfa fields was recorded. Various factors apparently influencing haystack depredation were noted.

Evidence of the failure of hunting seasons to control this herd are noted and some reasons for this failure are presented.

LITERATURE CITED

AMERICAN JOINT COMMITTEE ON HORTICULTURAL NOMENCLATURE. 1942. Standardized plant names. J. Horace McFarland Company, Harrisburg, Pa. 675pp.

BISSELL, HAROLD D., BRUCE HARRIS, HELEN STRONG, AND FRANK JAMES. 1955. The digestibility of certain natural and artificial foods eaten by deer in California. Calif. Fish and Game, 41:57-78.

BOOTH, W. E. 1950. Flora of Montana, part I, conifers and monocots. Research Foundation at Montana State College, Bozeman, Mont. 232pp.

COLE, GLEN F. 1956. The pronghorn antelope—its range use and food habits in central Montana with special reference to alfalfa. Mont. State Coll. Expt. Sta. Bull. 516, 63pp.

DOMAN, EVERETT R., AND D. I. RASMUSSEN. 1944. Supplemental winter feeding of mule deer in northern Utah. J. Wildl. Mgmt., 8:317-338.

HORMAY, AUGUST L. 1943. Bitterbrush in California. Calif. Forest and Range Expt. Sta., Res. Note No. 34, 13pp.

INTERSTATE DEER HERD COMMITTEE. 1951. The Devils Garden deer herd. Calif. Fish and Game, 37:233-272.

LASSEN, ROBERT W., CARROL M. FERREL, AND HOWARD LEACH. 1952. Food habits, productivity and condition of the Doyle mule deer herd. Calif. Fish and Game, 38:211-224.

LEOPOLD, ALDO. 1933. Game management. Charles Scribner's Sons, New York, N.Y. 481pp.

———, LYLE K. SOWLS, AND DAVID L. SPENCER. 1947. A survey of over-populated deer ranges in the U.S. J. Wildl. Mgmt., 11:162-177.

MARTIN, A. C., R. H. GENSCH, AND C. P. BROWN. 1946. Alternative methods in upland game-bird food analysis. J. Wildl. Mgmt., 10:8-12.

NORRIS, J. J. 1943. Botanical analysis of stomach contents as a method of determining forage consumption of range sheep. Ecology, 24: 244-251.

ROGERS, GLENN E. 1953. Function and operation of big-game check stations in Colorado. J. Wildl. Mgmt., 17:256-267.

SAUNDERS, JACK. 1955. Food habits and range use of the Rocky Mountain goat in the Crazy Mountains, Montana. J. Wildl. Mgmt., 19: 429-437.

SMITH, ARTHUR D., AND RICHARD L. HUBBARD. 1954. Preference ratings for winter deer forages from northern Utah ranges based on browsing time and forage consumed. J. Range Mgmt., 7:262-265.

SMITH, JUSTIN G. 1952. Food habits of mule deer in Utah. J. Wildl. Mgmt., 17:101-112.

THOMAS, D. WOODS, AND JEROME K. PASTO. 1955. A theoretical framework for understanding the deer management problem. J. Wildl. Mgmt., 19:143-147.

WRIGHT, J. C., AND W. E. BOOTH. 1956. Flora of Montana, Dicotyledons. Herbarium of Montana State College. 226pp.

Received for publication July 11, 1956.

WEIGHT AND BODY-FAT RELATIONSHIPS OF MOURNING DOVES IN ILLINOIS

Harold C. Hanson and Charles W. Kossack

Illinois Natural History Survey, Urbana, Illinois

The physiological responses of wild birds to the stimuli that induce migration have received increasingly intensive study in recent years. Of the various manifestations of readiness to migrate fat deposition has been singled out by Wolfson (1942, 1945, and 1954) and others as being of particular importance.

An opportunity to study this relationship in the mourning dove (*Zenaidura macroura*) was provided by an investigation of this species in Illinois between 1948 and 1954. Findings in this report are based almost entirely upon study of doves in the wild, thereby differing from those of many previous investigations that have relied chiefly upon results of experiments with caged individuals. Our data offer information on rates of deposition of fat in the immature of a species that increases its body weight and continues the process of physical maturation for ten weeks after leaving the nest. The role of deposition of fat in young doves is also complicated by the occurrence of a complete body molt and the initiation of migrational movements during this period of growth.

MATERIALS AND METHODS

The data presented here are on a sample of over 600 doves taken chiefly during the

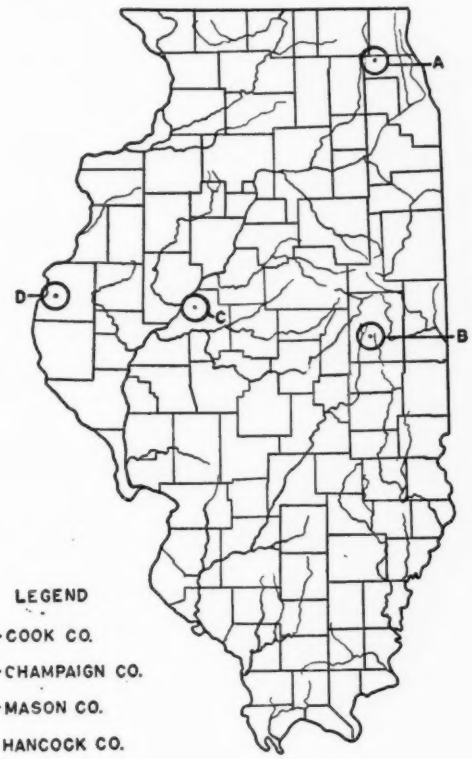


FIG. 1. Principal areas in Illinois where mourning doves were collected.

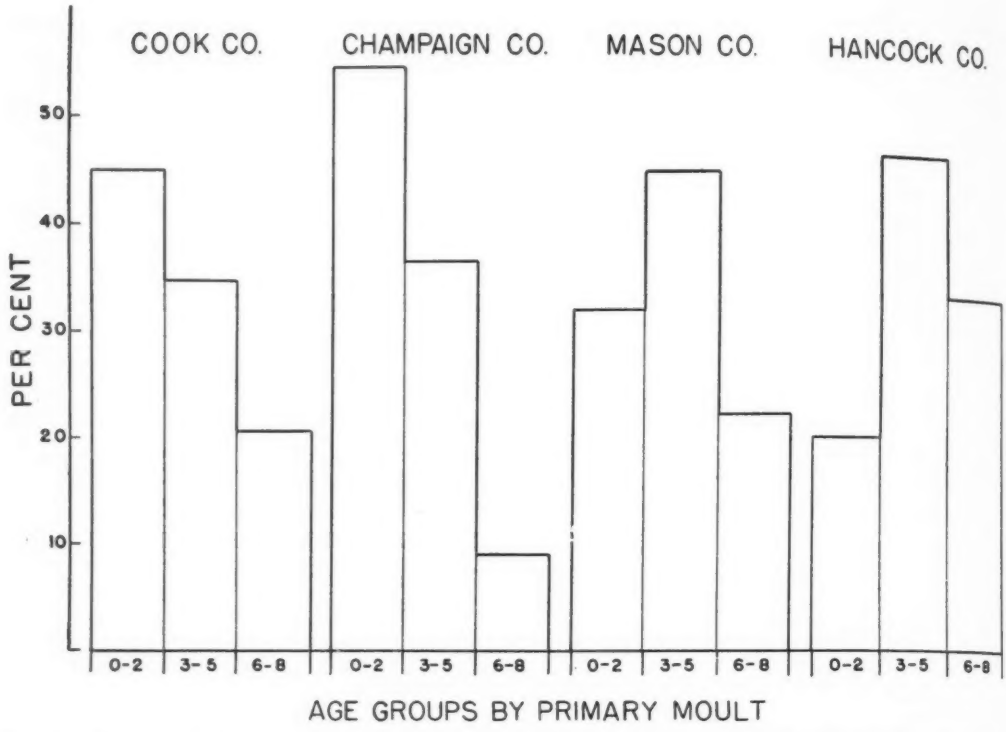


FIG. 2. Frequency of age groups of immature doves by combined categories of primary-molt groups.

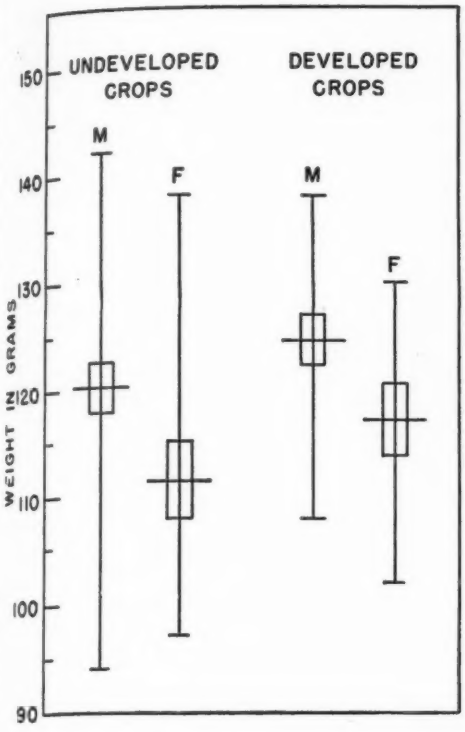
Illinois hunting season, September 1-30. A few, however, were collected in July and August. The counties where collections were made are shown in Fig. 1. Collected doves were weighed during the evening of the day they were shot, or kept on ice and weighed the following day. The stage of molt of the wing primaries, i.e., the primary most recently lost or in the process of being replaced, was recorded. Recorded body weights were corrected by subtracting the weight of the crop contents. This correction was important as the crop contents of these doves weighed as much as 11 grams, or 8-10 per cent of the actual body weight. The doves were then plucked and, on the basis of examination and dissection, the relative amount of body fat was estimated, using the McCabe scale (1943). For convenience, numerals 1-6 were assigned to the various categories: 1—*no fat*, 2—*little fat*, 3—*moderate fat*, 4—*fat*, 5—*very fat*, and 6—*excessively fat*. The use of figures had the advantage that average fat values could be calculated for comparative purposes. In some cases fat classes were combined in order to present a simpler and clearer presentation. Sex and breeding condition were determined by dissection.

For assistance in collecting specimens, we wish to acknowledge especially the help of George C. Arthur of the Illinois Department of Conservation, and of Milo, John and Donald Suchy, and George Wold of Barrington, Illinois. Kossack (1952) has described the procedure used in obtaining specimens from hunters in the Barrington, Illinois, region. We are indebted to Albert Wolfson, Northwestern University, with whom the data were discussed at an early stage of the study, and to S. Charles Kendeigh, University of Illinois, for helpful criticism of the manuscript. H. W. Norton of the University of Illinois provided helpful advice on statistical matters.

RESULTS

Regional Differences in Age of Immature Doves

The ages of the immature doves showed surprising regional differences: those col-



		UNDEVELOPED CROPS		DEVELOPED CROPS	
MALES	N	73		67	
	M	121.6	1.6	123.6	1.1
	S.D.	13.2	1.1	9.4	0.8
	V	10.9	0.7	7.6	0.7
FEMALES	N	55		40	
	M	111.6	1.3	117.6	1.2
	S.D.	9.5	0.9	7.6	0.8
	V	8.5	0.8	6.5	0.7

FIG. 3. Mean and extreme weights of adult mourning doves with undeveloped and developed crops. Rectangles in graph represent limits of two times the error of the mean above and below the mean. Each datum in the table below the figure is followed by its standard error.

lected in Champaign County averaged least in age, followed by birds from Cook and Mason counties with a markedly higher percentage of older immatures being collected in Hancock County, Fig. 2. Age differences might be expected to be greatest between northern and central Illinois collecting stations because of the 150-mile difference in latitude, the corresponding climatic differences, and the possibility of correlative differences in the nesting phenology, but the greatest age differences were found between collections of immature individuals from east-central and west-central Illinois.

Body Weight of Doves

Sex and age differences.—Weights of adult mourning doves from the four study areas are summarized in Fig. 3. In both sexes the average weights of birds that showed development of the crop pads were greater than those of birds that were not undergoing a similar phase of a reproductive cycle at the time of collection. In the males the difference is 1.6 per cent; in the females, 5.4 per cent. The greater and statistically significant difference between the females is accounted for in part by the increased development of the ovary and particularly the oviduct, which is partially synchronized with the development of the crop pads.

Body-weight data for nine age categories of immatures from the four areas are summarized in Fig. 4. In each category, the average weight of the males significantly exceeds that of the females, the males averaging 8.5 per cent heavier than the females with the difference varying from 5.8 to 10.8 per cent. Our data indicate that the immatures attain a body weight equal to the adults when they are about midway between the molt of their sixth and seventh primaries (Figs. 3 and 4). However, total body-weight comparisons alone are misleading without reference to body fat. For a brief period, between the molting of primaries 7 and 8, some immatures carry a heavier fat load than the adults and hence exceed average weights for adults not in breeding condition.

Regional weight differences.—It might be assumed that a common, widespread, and highly migratory species such as the mourning dove would show little geographic variation in body weight over so small a part of its total range as Illinois. Yet some regional weight differences were noted (Tables 1 and 2). Immature doves collected in Hancock County averaged significantly heavier in most age groups than immature doves collected in the other three state areas.

TABLE 1. — MEAN AND EXTREME WEIGHTS OF JUVENILE MALE MOURNING DOVES IN ILLINOIS IN RELATION TO AREAS OF COLLECTION

Age by Primary Molt	Cook Co. Number	Mean	Range	Champaign Co. Number	Mean	Range	Mason Co. Number	Mean	Range	Hancock Co. (1952) Number	Mean	Range	Hancock Co. (1952-53) Number	Mean	Range
0	12	92.5	81.2-108.4	1	103.7	——	1	115.7	——	2	99.8	88.0-111.6	2	99.8	88.0-111.6
1	19	99.7	75.9-124.5	6	104.4	96.0-120.2	3	107.0	94.5-114.5	3	110.6	102.8-123.5	5	106.5	102.8-123.5
2	24	106.4	88.5-128.0	0	(105.8)*	——	3	115.8	107.5-123.0	6	111.2	96.3-134.4	12	107.9	94.0-134.4
3	23	112.1	90.0-125.9	9	107.2	95.7-114.8	6	113.1	101.6-123.8	9	119.9	103.0-149.6	17	114.9	102.0-149.6
4	15	113.4	102.0-121.1	2	121.9	118.3-125.6	2	108.7	99.6-117.7	5	127.8	117.5-131.7	10	120.3	98.3-134.2
5	5	112.5	98.0-120.7	0	(120.7)*	——	4	117.0	105.7-120.6	5	124.1	112.5-129.8	6	126.3	112.5-137.5
6	5	110.2	90.6-125.5	5	119.5	105.5-137.8	5	120.8	113.4-129.7	6	129.8	121.2-148.7	16	132.2	109.9-150.8
7	1	125.3	——	5	131.4	118.2-147.6	1	95.4	——	5	129.2	119.4-138.0	6	126.0	110.1-138.0
8	1	121.6	——	1	116.3	——	1	106.5	——	4	122.8	114.0-127.9	6	123.0	114.0-129.0
Totals	105			29			26			45			80		
Averages		110.4			114.5			111.1			119.5			117.4	

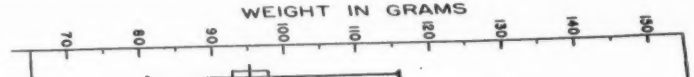
*Data represent midpoints between the preceding and following weights. These were included so that an over-all average could be calculated.

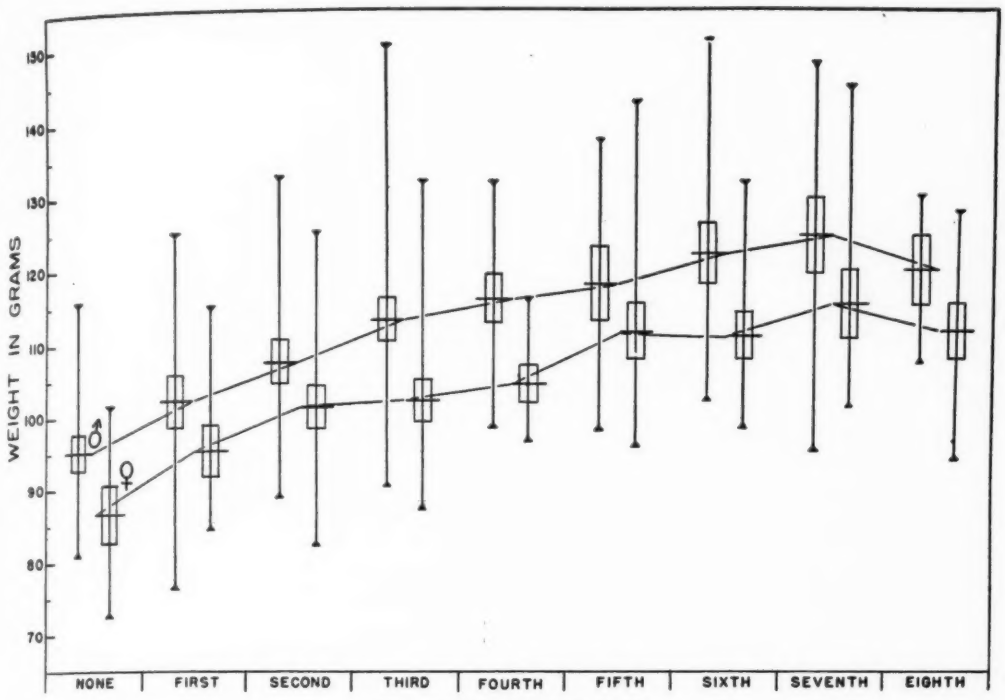
TABLE 2. — MEAN AND EXTREME WEIGHTS OF JUVENILE FEMALE MOURNING DOVES IN ILLINOIS IN RELATION TO AREAS OF COLLECTION

Age by Primary Molt	Cook Co. Number	Mean	Range	Champaign Co. Number	Mean	Range	Mason Co. Number	Mean	Range	Hancock Co. (1952) Number	Mean	Range	Hancock Co. (1952-53) Number	Mean	Range
0	10	84.2	70.1-100.5	3	83.6	75.5-91.3	1	101.8	——	2	93.3	88.9-98.0	4	90.7	86.2-98.0
1	7	96.6	88.0-114.7	3	91.8	89.3-96.2	1	93.9	——	2	93.5	87.9-99.2	6	93.3	84.0-104.8
2	12	101.7	90.3-113.9	4	100.7	99.8-103.4	7	102.3	93.0-110.5	4	104.2	100.8-110.6	9	100.1	85.3-124.9
3	7	102.9	88.7-108.1	6	101.3	92.5-110.9	6	104.9	99.4-112.5	7	106.4	89.7-132.2	19	101.0	89.7-132.2
4	7	108.2	97.8-118.7	6	103.5	91.5-111.4	1	93.2	——	2	112.7	109.9-115.5	8	103.7	87.4-115.5
5	7	108.7	78.9-124.8	7	107.6	97.5-118.6	5	110.2	97.5-113.9	7	120.6	103.3-127.4	17	115.0	96.4-143.0
6	9	110.5	101.4-120.4	2	117.1	110.6-123.6	4	112.1	101.7-131.5	2	111.4	111.3-111.5	7	110.0	98.3-123.2
7	10	113.7	102.4-124.6	2	117.0	108.4-125.5	2	108.8	103.7-113.9	5	128.0	105.5-145.4	9	117.8	101.2-145.4
8	4	112.3	97.8-120.3	4	118.2	113.6-127.2	2	103.9	93.6-114.1	4	115.9	105.4-127.9	11	111.5	102.0-127.9
Totals	73			37			29			35			90		
Averages		104.3			104.5			103.5			109.6			104.8	

Age c
shown
Illinois
averag
stages
shown
matures
edly ir
state re
habits.
the rat

Fig. 4.
mary-mo
times th





		NONE	FIRST	SECOND	THIRD	FOURTH	FIFTH	SIXTH	SEVENTH	EIGHTH
MALES	N	19	34	40	56	31	17	34	22	10
	M	95.3 1.2	102.3 1.9	107.6 1.5	112.5 1.5	115.7 1.6	118.1 2.5	122.2 2.0	124.6 2.5	119.7 2.4
	S.D.	5.1 0.8	10.9 1.3	9.7 1.0	11.2 1.1	8.7 1.1	10.3 1.8	11.5 1.4	11.5 1.7	7.7 1.7
	V	5.4 0.9	10.7 1.3	9.0 1.1	10.0 0.9	7.5 0.9	8.7 1.5	9.4 1.1	9.2 1.4	6.4 1.4
FEMALES	N	20	20	36	38	24	40	26	23	20
	M	86.9 2.0	94.5 1.8	101.0 1.4	101.8 1.5	104.4 1.3	111.6 1.9	111.0 1.6	115.3 2.3	111.7 1.9
	S.D.	9.0 1.0	7.9 0.9	8.7 1.0	9.3 1.1	6.6 1.0	12.1 1.4	8.4 1.2	10.9 1.6	8.6 1.4
	V	10.4 1.2	8.4 0.9	8.6 1.0	9.1 1.0	6.3 0.9	10.9 1.2	7.5 1.0	9.4 1.4	7.7 1.2

FIG. 4. Mean and extreme weights of male and female immature mourning doves in successive primary-molt age classes. The rectangle about the mean value represents the limits for the value of two times the error of the mean above and below the mean. In the accompanying table, each datum is followed by its standard error.

Body-fat Relationships

Age and regional differences.—It has been shown that immature dove populations in Illinois in September varied regionally in average age and in weight at successive stages of molt of primaries. It can further be shown that the rate of gain of body fat of immature doves in September may vary markedly in some years in restricted areas of a state region as a result of specialized feeding habits. In Fig. 5, comparison is made of the rates of gain of fat by different primary-molt age groups of immature doves shot in September. The patterns of gain of fat of immature doves from Cook and Champaign counties were so similar that data for those doves were combined. Immatures collected in Hancock County in 1952 and 1953 were considerably heavier than those collected in any of the other three state areas. The greater weights of the Hancock County doves were apparently chiefly due to their greater fatness.

The percentage of doves that carry various amounts of body fat is also of considerable

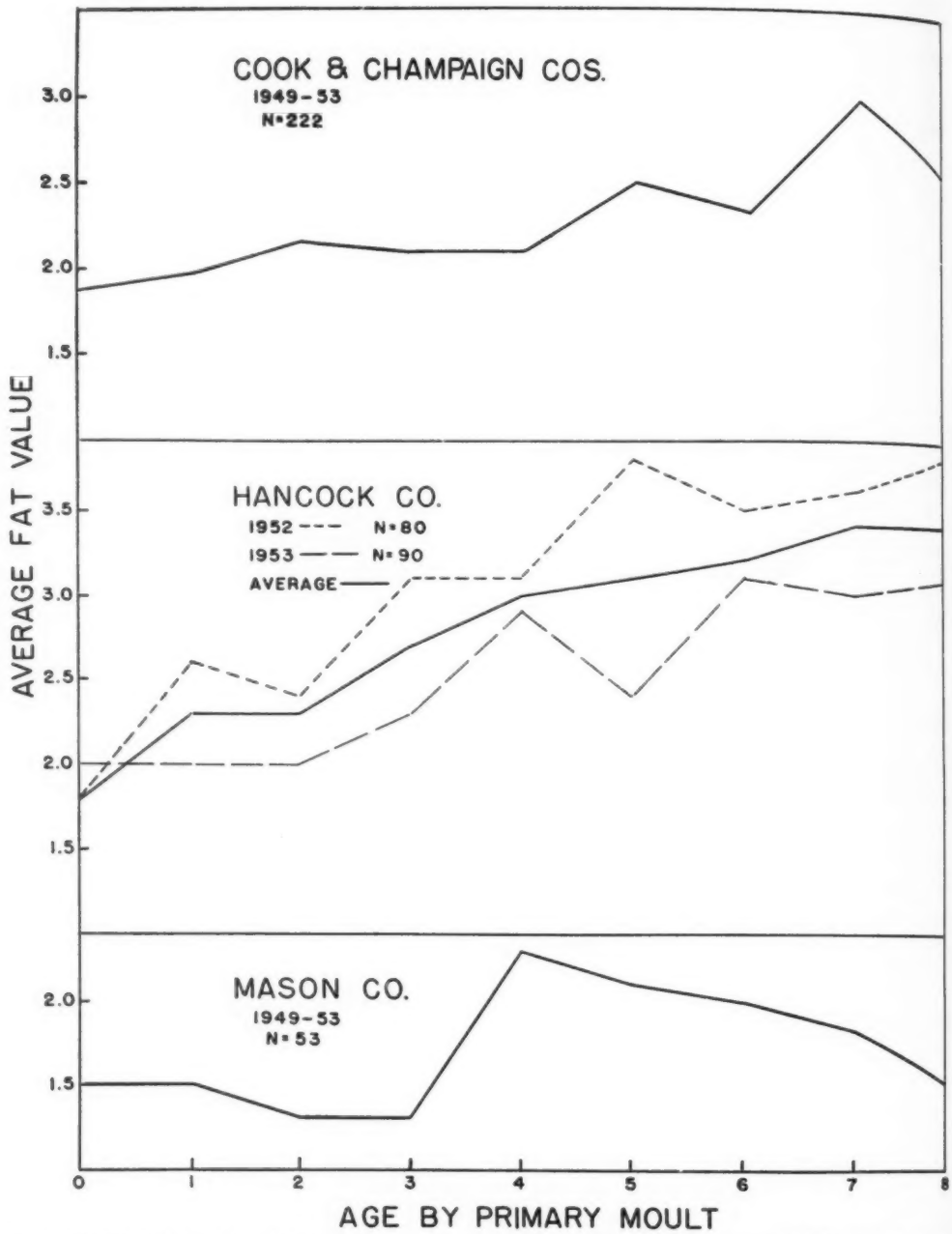


FIG. 5. Average fat values for immature mourning doves collected in four areas of Illinois. Curve plottings are by successive primary-feather molt.

interest. These data are summarized by primary-molt age groups and by counties in which the doves were collected, Fig. 6. For this analysis, *moderately fat* includes moderate fat (class 3) and fat (class 4) birds; *very fat* represents very fat (class 5) and excessively fat (class 6) birds.

Weight differences.—The amount of fat carried by immature doves was reflected in their average body weight (Tables 3 and 4).

TABLE 3. — MEAN AND EXTREME WEIGHTS OF IMMATURE MALE MOURNING DOVES IN ILLINOIS BY PRIMARY-MOLT AND FAT CATEGORIES, 1948-53

Age by Primary Molt	No Fat (Category 1)			Little Fat (Category 2)			Moderately Fat (Categories 3 and 4)			Very Fat (Categories 5 and 6)		
	No.	Mean	Range	No.	Mean	Range	No.	Mean	Range	No.	Mean	Range
0	6	95.7	81.2-111.6	3	95.8	92.0-115.7	2	98.4	94.5-102.4	0	—	——
1	11	108.0	90.2-114.5	10	107.9	94.5-124.5	3	104.0	100.7-108.4	2	121.9	120.2-123.5
2	7	104.6	91.6-115.3	10	105.7	94.0-123.0	5	112.7	105.0-134.4	1	113.2	——
3	12	107.3	90.0-118.1	22	111.1	101.1-126.0	11	111.5	95.7-134.1	3	140.2	134.7-149.6
4	8	109.6	102.0-119.5	8	111.8	98.3-123.3	8	118.4	110.5-125.6	3	132.0	130.0-134.2
5	0	—	——	8	116.8	105.7-126.2	5	119.6	98.0-129.8	1	137.5	——
6	3	105.9	101.9-110.4	16	119.0	109.9-129.7	7	121.6	111.7-137.8	4	142.8	135.5-150.8
7	1	95.4	——	5	118.6	110.0-129.2	12	126.8	118.2-142.6	3	139.9	134.0-147.6
8	1	106.5	——	2	115.6	114.0-116.3	5	123.2	117.9-129.0	1	129.8	——

Immature doves rated as having "little fat" carried such small amounts of fat that it seems probable that part of the weight difference between these doves and those rated as carrying "no fat" represents the more complete development of the skeletal musculature of the former. Mason County birds appeared to be more poorly "fleshed" than immatures collected elsewhere in the state and many were so devoid of fat that their skin, when plucked of feathers, had a bluish appearance. Despite the marked variability of weights in the various age and fat categories, fairly consistent differences were found between the average weights for each fat category within specific primary-molt age groups.

The average of mean weights of immature doves in all the nine primary-growth stages in each of the "fat" categories exceeded the average weight of doves carrying no body fat by the following: males—little fat 7.0 per cent, moderately fat 10.6 per cent, and very fat 27.0 per cent; females—little fat 5.8 per cent, moderately fat 14.6 per cent, and very fat 23.5 per cent. However, if a comparison is made only between the older molt-age classes, those in the "very fat" class will be found to exceed the average weight of doves of comparable age carrying no body fat by as much as 30-35 per cent. These average-weight differences between birds of different fat categories are similar to those reported for transient white-throated sparrows (*Zonotrichia albicollis*) by Wolfson (1954).

DISCUSSION

Regional Differences in Age of Immature Doves

Possibly a number of doves reared in adjacent areas of bordering states, particularly in Wisconsin, were included in the samples studied; of the doves collected in Hancock County, a few may have originated in eastern Minnesota and Iowa. The heaviest kills of doves per hunter were made in counties that bordered the major rivers and their main

TABLE 4. — MEAN AND EXTREME WEIGHTS OF IMMATURE FEMALE MOURNING DOVES IN ILLINOIS BY PRIMARY-MOLT AND FAT CATEGORIES, 1948-53

Age by Primary Molt	No Fat (Category 1)			Little Fat (Category 2)			Moderately Fat (Categories 3 and 4)			Very Fat (Categories 5 and 6)		
	No.	Mean	Range	No.	Mean	Range	No.	Mean	Range	No.	Mean	Range
0	5	81.8	70.1-91.3	8	92.7	86.2-101.8	0	—	——	1	83.9	——
1	7	90.5	84.0-96.2	6	94.1	87.9-99.2	4	100.9	94.0-109.5	0	—	——
2	10	97.4	91.1-100.8	13	99.4	88.9-110.5	8	104.2	93.0-110.6	1	124.9	——
3	10	99.7	88.7-107.9	17	98.4	86.9-112.5	8	104.9	99.0-117.4	2	126.0	119.8-132.2
4	3	96.6	91.5-99.6	10	105.4	87.4-118.7	6	105.9	93.2-112.7	0	—	——
5	3	95.5	78.9-107.2	12	106.1	96.4-117.3	8	114.5	103.4-121.3	10	126.2	118.6-143.0
6	3	103.7	101.7-107.2	6	111.7	99.6-129.7	9	112.0	98.3-131.5	1	123.2	——
7	1	103.7	——	13	110.9	101.2-125.5	4	117.9	111.5-124.6	3	135.3	125.7-145.4
8	2	104.7	93.6-115.7	1	105.3	——	1	130.0	——	0	—	——

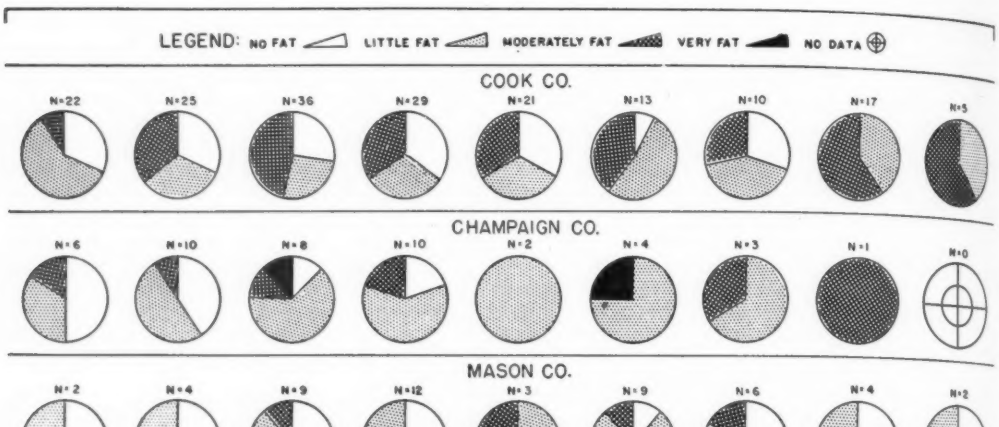

LEGEND: NO FAT LITTLE FAT MODERATELY FAT VERY FAT NO DATA
COOK CO.
N=22 N=25 N=36 N=29 N=21 N=13 N=10 N=17 N=5
CHAMPAIGN CO.
N=6 N=10 N=8 N=10 N=2 N=4 N=3 N=1 N=0
MASON CO.
N=2 N=4 N=9 N=12 N=3 N=9 N=6 N=4 N=2
HANCOCK CO.
N=6 N=11 N=17 N=36 N=19 N=24 N=25 N=15 N=17
NONE FIRST SECOND THIRD FOURTH FIFTH SIXTH SEVENTH EIGHTH
AGE GROUPS BY PRIMARY MOULT

FIG. 6. Frequency of immature doves in four fat categories in relation to age and state areas. Years represented by data: Cook Conty 1951 and 1952; Champaign County 1948-53; Mason County 1948-53; and Hancock County 1952 and 1953.

tributaries (Hanson and Kossack, 1950). By virtue of superior nesting habitat and abundant water supply, these counties harbor a relatively high population of nesting doves as well as attract a concentration of migrating doves during fall. Thus, both locally reared and migrant doves were believed to be represented in the samples. While the normal fall migration movements in the state are mainly southward, the pattern of drainage may tend to channel flights toward the southwest. These factors may partially explain the disparity in age of immatures found between our collections for the four counties representing regions in different parts of Illinois (Fig. 1).

Correlation of the peaks of hatching and of peaks and lows in weekly roadside censuses made in northeastern Illinois indicated that the early-hatched young begin local movements or migrate from their home territory from early to mid-July when they are five or six weeks of age. This finding is in agreement with that of McClure (1943), who has stated that migration in doves began with the movement of young in July. A few doves may even move northward in midsummer before their flights gradually transform into a southward migration. On the basis of extensive banding in Illinois, Taber (1930) concluded that doves migrate southward at the minimum rate of 6 to 13 miles per day. However, as this calculation is based on the interval between banding and time of recovery, it has little meaning in terms of the distances covered in single flights. Spells of cooler weather in August appeared to accentuate movements, but roadside counts (Fig. 7) demonstrated that, in any event, the locally reared population in the northern part of the state decreased after about mid-August. The flocking and southward movements of the older age groups, i.e., of early-hatched immature doves, from the northern areas of Illinois and Wisconsin as well, in effect reduce the average age of the immature population remaining behind. Data in Fig. 2 also appear

to bear this out, a higher percentage of older immatures being found in the counties that lie adjacent to the Illinois and Mississippi rivers.

Body-weight Relationships

Our data show that adult mourning doves having fully developed crops and oviducts average greater in weight than those not showing some degree of development of these organs. The difference, however, was not so great as that reported for the ring dove (*Streptopelia risoria*), the reason being that only a relatively few adult mourning doves collected while in a phase of the breeding cycle were taken when the reproductive organs were at peak development. Riddle and Braucher (1934) have shown that the body weight of female ring doves is increased 2-3 per cent by the marked (1,000 per cent) and temporary growth of the oviduct. During the last four days of incubation, the body weight of adult breeding ring doves increases by 7.7 per cent, the great temporary increase of the crop glands accounting for one-third of this increase.

Our weight data reveal that male immature doves average significantly heavier than the females in each of nine successive growth and primary-molt age stages.

Body Fat in Immature Doves

Regional differences.—Regional differences in the rate of gain of fat in immature doves were indicated by the samples. Immature doves from Hancock County put on considerable amounts of body fat during the early stages of primary molt and during the peak of the body molt even when the body growth was still proceeding at a fairly rapid pace. In contrast, the immature doves from Mason County did not gain an appreciable amount of body fat *regardless of age*. These facts indicate that deposition of fat in mourning doves is not wholly under inherent, internal control, but is dependent on a variety of external environmental factors.

Effect of soils.—Soil fertility offers a partial, though indirect, explanation as to why doves fatten more readily in one area than in another, but in view of the seemingly greater importance of other factors, only the briefest characterization of the soils concerned seems appropriate. Those of the general region of Barrington in Cook County vary from fairly thin woodland soils over a heavy layer of highly porous glacial drift to fertile heavy prairie soils in the lower more level areas (Wascher and Odell, 1951). About 92 per cent of Champaign County is

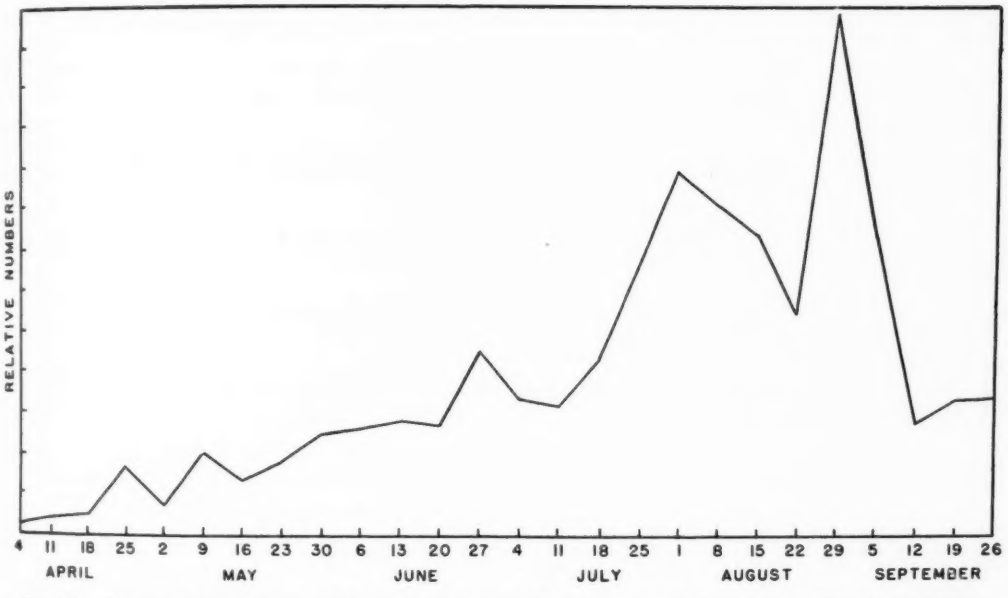


FIG. 7. Seasonal trend in roadside counts of mourning doves near Barrington, Illinois, 1949-52.

covered by upland prairie soils classified for the most part as "brown silt loam" (Hopkins, *et al.*, 1918) and of outstanding fertility. About 68 per cent of the soils of Mason County are sandy, and low in nitrogen and organic matter (Smith, *et al.*, 1924b). Extensive areas are covered by dunes which support only a sparse vegetation. Cultivated soils in Hancock County are equally divided into two main types: upland prairie soils, 45 per cent; upland woodland soils, 45 per cent (Smith, *et al.*, 1924a). In terms of yield of corn per acre, Hancock County soils are comparable to those of Cook County.

The farming practices of the regions are correlated with soils. Cook County, in the region where collecting was done, is devoted chiefly to dairy farming with some general farming and stock feeding. Champaign County is devoted to cash-grain crops (corn and soybeans). Mason County lies in a mixed farming area devoted mainly to cash-grain crops and Hancock County lies in a region of the state where livestock and grain furnish the principal income. The farming practices in the latter county differ notably from those of the others in that hogs are often fed in large lots or open fields where corn is scattered on the ground.

Effect of food habits.—The food habits of the doves taken in the four counties reflected the soil types, soil fertility, and local farming practices. Wheat, seeds of foxtail grass, and various weeds were the principal foods eaten in Cook County. Doves taken in Champaign County had similar food habits, although corn was a more important item of diet. Weed seeds formed the chief diet of doves in Mason County, with *Croton* sp., appropriately named "dove weed," being a characteristic food. Corn was a relatively unimportant food. In Hancock County, all of the doves collected in 1952 were shot in the vicinity of hog-lots or in flight in late afternoon enroute from hog-lots to hedgerow roosts. With few exceptions, the crops of these birds contained chiefly corn. In 1953, part of the collection was comprised of "hog-lot doves," but the larger part consisted of doves that were literally fleeing southward with the advance of a cold front that broke a long hot spell. While the majority of these latter doves had empty crops, the distance they had flown prior to the time of collection (4:00-6:00 P.M.) was unknown. A number of doves were also shot at a hog-lot. The mixed character of the 1953 collection was reflected in the weights (and fatness) of the individuals, both unusually light and exceptionally heavy birds being taken (Tables 1 and 2). John C. Oberheu, Cooperative Wildlife Research Laboratory, Southern Illinois University, who made a detailed study of the 1952-54 crops collected in Champaign, Mason, and Hancock counties, kindly provided us with information on the six ranking foods, based on frequency of occurrence and volume (Table 5).

Considered on the basis of the volumetric percentage of cultivated foods found in the dove crops, the correlation of foods with body weight and amounts of body fat is particularly good. Analyses by Mr. Oberheu showed that in Hancock County 89 per cent of the food by volume consisted of cultivated species, as compared with 51 per cent in Champaign County and only 38 per cent in Mason County.

The fatness of the Hancock County birds collected in 1952 and part of 1953 was so marked and atypical of populations sampled elsewhere in the state that it was deemed desirable to examine immature doves from this county again in 1954 and 1955. In these

TABLE 5.—THE SIX RANKING FOODS OF MOURNING DOVES IN THREE COUNTIES IN ILLINOIS, 1948-53

Rank	Champaign County	Mason County	Hancock County
1	Foxtail grass (*Setaria*)	Foxtail grass (*Setaria*)	Corn (*Zea mays*)
2	Wheat (*Triticum aestivum*)	Croton (*Croton*)	Foxtail grass (*Setaria*)
3	Corn (*Zea mays*)	Crab-grass (*Digitaria*)	Wheat (*Triticum aestivum*)
4	Spurges (*Euphorbia*)	Wheat (*Triticum aestivum*)	Crab-grass (*Digitaria*)
5	Crab-grass (*Digitaria*)	Panic-grass (*Panicum*)	Spurges (*Euphorbia*)
6	Panic-grass (*Panicum*)	Lesser ragweed (*Ambrosia artemisiifolia*)	Panic-grass (*Panicum*)

seasons, smaller collections were made by "pass shooting" carried out in an area away from hog-lots. These doves had fed almost exclusively on the seeds of foxtail grass (*Setaria* sp.) and were found to be similar in fatness to doves collected in Cook and Champaign counties.

Lack of fatness in mourning doves may be related not only to poor soils but also the kind and nutritive value of foods eaten. Unusual fatness in immature doves also appears to be a regional phenomenon to the extent that locally feeding segments of a population develop a specific food habit as a result of local agricultural practices. According to George C. Arthur, a resident of Hancock County, each year flocks of doves establish the habit of feeding in hog-lots at least several weeks in advance of the hunting season. Having an abundance of fattening food and little inducement to seek food elsewhere or to migrate, these "baited," local populations would be capable of putting on fat at a faster rate than doves in migration. Elsewhere in the state, dove flocks in late summer shift about locally, following the harvest of small grains and the seeding of winter grain crops.

The rate of gain of fat shown by immature doves from Cook and Champaign counties, where the doves have generalized feeding habits, is believed to be representative of that of the greater bulk of the immature dove population in Illinois in September. This opinion is also based on the degree of fatness of doves in Hancock County that were not dependent on hog-lot corn and a small collection of doves from southern Illinois. The extreme low and high gains of fat of doves from Mason and Hancock counties, where local situations are reflected, are not regarded as typical of the Illinois population as a whole.

The inability of immature doves from Cook and Champaign counties to gain fat in the period between the molt of the second and fourth primaries (Fig. 6) is believed to reflect the stress of rapid growth at these ages. Data plotted for some years show a distinct trough in the rate of gain of fat during the molt of the third primary. Study of a series of skins and notes on plumage taken at autopsy showed that the molt of the body feathers begins at the time of molt of the second primary wing feathers, is at its height during the molt of the third, and is essentially complete by the time of the molt of the fifth wing primary. The rate of gain in total body weight also drops during the body molt, and this is believed to be a direct expression of this stress, as the molt of body feathers is undoubtedly accompanied by an accelerated rate of loss of heat. The replacement of the feathers is also an energy-demanding process of considerable magnitude. These two factors, which possibly also result in a higher metabolic rate at this period, are regarded as sufficient to explain the drop in the rate of body weight and body fat gain during the body molt. Studies of poultry have shown that the metabolic rate of hens during the molt is increased about 50 per cent (Sturkie, 1954, p.147). Richdale (1947) has pointed out that a number of species are known to lose weight during the molt whereas others do not. Captive Canada geese (*Branta canadensis interior*) lost weight during the period of regrowth of the wing feathers (Hanson, unpublished).

Fat deposition and migration.—The role of deposition of fat in relation to migration has been clarified and emphasized by Wolfson (1942, 1945, and 1954) and later by Blanchard and Erickson (1949), Odum and Perkinson (1951), and others. From his studies on juncos (*Junco oreganus*), Wolfson (1942, 1945: 112) maintains that "deposition of fat precedes migration and that without this 'preparation' migration is usually not undertaken." He believes (1945:122) that it is "best to regard fat deposition as a primary part of a general, metabolic internal stimulus and as an excellent indicator of readiness to migrate."

Our findings indicate that in most areas of the state doves do not put on appreciable quantities of fat (No. 3 or "fat") until the molt of the fifth wing primary (Fig. 8). Although perhaps many of the doves shot prior to this molt stage were resident birds, it would appear from findings at hand that many young doves begin their southward journey before putting on much fat. The apparently leisurely movements of doves at the beginning of their migration in late summer when the weather is warm and when food supplies are abundant suggest that they do not have an initial *need* for a large fat reserve, although, where high-quality foods

are available in abundance (in regions such as Hancock County), they are capable of putting on large amounts of fat even at an early age and stage of growth.

Without exceptions, the doves collected in Mason County carried little or no body fat. These doves would have almost necessarily migrated before being able to put on body fat, as the great majority of the doves in this region leave by mid-September. On the other hand, many doves in some areas of Hancock County leave for the south with considerable fat. It might be argued that a larger percentage of the doves shot in Hancock County are migrants already physiologically ready for fat deposition. Refutation of this hypothesis is suggested by differences between (a) the fat data for Hancock County doves for the years 1952 and 1953 (Fig. 5) and the smaller collections made in 1954 and 1955, and (b) the finding that doves collected in other areas of the state did not put on appreciable amounts of fat until the molt of their fifth primary.

Body Fat in Adult Doves

The preceding discussion has referred to immature doves. Adult doves collected in September seldom carry large amounts of fat regardless of area of origin. Few individuals rated higher than "fat" on the McCabe scale. The average fat scale of 266 adults was 2.8. No difference was found in average fat values between adults with developed crops and those with crop pads showing no development.

Utilization of Energy in Doves

Kendeigh (1949) has advanced the concept that "birds make the most efficient use of their productive energy by the spacing of their major activities so that they do not occur simultaneously or seriously overlap... One activity does not ordinarily begin until the previous one is completed...." However, such spacing of major energy-demanding activities is not clear-cut in doves. Young doves collected in September in various stages of molt may or may not carry appreciable amounts of body fat, apparently depending largely on the kinds of food available. The complete molt undergone by young doves soon after leaving the nest may partially explain the relatively long time required for them to reach adult weight. Furthermore, adult doves complete their nesting cycle while in the molt and initiate migration while in the latter stages of the molt; this is indicated by the fact that, of the adult wild doves autopsied by us found to be in breeding condition or with a developed crop, none had molted more than the seventh primary. This has also been supported by the recovery of dyed feathers from our breeding captive doves. Most adults showing a developed crop pad were in the process of replacing the sixth primary. Because considerable energy is used for molt, part of which occurs during the migration period and part, in adults, during nesting, doves do not appear to have the physiological efficiency of higher types of birds.

Stimulus for Migration

We have repeatedly noted that, whereas doves are relatively tame during most of the spring and summer, they begin to exhibit a restlessness and wildness when they gather into flocks in late summer. The restlessness of dove flocks in late summer is here construed as an outward manifestation that the birds are in "Zugdisposition," i.e., in the physiological state of readiness to migrate (Farner, 1950; Eyster, 1954) during which period an external stimulus is needed to set migration in motion. The sensitivity of mourning doves to temperature changes in the autumn, as shown by the timing of their movements, underlies the importance of sharp changes of temperature as an immediate stimulating factor in this species.

SUMMARY AND CONCLUSIONS

The average age and the frequency of molt-age classes of immature doves varied in collections from different regions of Illinois. Greatest average differences in age were found between collections of doves from east-west stations (Champaign–Mason–Hancock counties); less important differences existed in the age of immature doves from two stations lying approximately directly north and south of each other (Champaign–Cook counties).

Roadside counts and age of immature doves by region indicated a gradual exodus of the young from their home sites after they attain the age of five or six weeks. The age

differences in doves between stations suggested that the late-summer movements over a large part of the state might tend to be somewhat southwestward, following the tributaries and river valleys. Differences in the average dates of nesting between localities were not adequate to account for regional differences in the age of late summer flocks.

Male mourning doves averaged significantly heavier in weight than females from at least several days prior to the loss of their first primary feathers in the postjuvenal molt through adult life.

A change in the rate of gain in body weight and gains in body fat during postjuvenile life appears to be associated with molting. This change was most pronounced in the period between the replacement of the second and fourth primary.

Correlations were found between regional differences in the rates of gain in body fat in immature doves and regional farming practices, soil fertility, and food habits.

Great gains of fat in mourning doves were associated with fertile soils and the availability of corn; low fat gains were associated with infertile, sandy soils, and a dependence on seeds of noxious weeds and native plants.

Adult doves collected in September usually carried only small or moderate amounts of body fat.

No consistent relationship was apparent between the amount of body fat, age, and migratory habits.

LITERATURE CITED

BLANCHARD, BARBARA N., AND MARY M. ERICKSON. 1949. The cycle in the Gambel sparrow. Univ. Calif. Publ. Zool., 47:225-318.

EYSTER, MARSHALL B. 1954. Quantitative measurement of the influence of photoperiod, temperature, and season on the activity of captive songbirds. Ecol. Monog., 24:1-28.

FARNER, DONALD S. 1950. The annual stimulus for migration. Condor, 52:104-122.

HANSON, HAROLD C., AND CHARLES W. KOSSACK. 1950. Flying acrobat gains in Illinois. Outdoors in Illinois (Ill. Dept. Cons. Mag.), 16: 30-31 (autumn issue).

HOPKINS, CYRIL C., J. G. MOSIER, E. VAN ALSTINE, AND F. W. GARRETT. 1918. Champaign County soils. Ill. Agric. Exp. Sta. Soils Rept. 18. 61pp.

KENDEIGH, S. CHARLES. 1949. Effect of temperature and season on energy resources of the English sparrow. Auk, 66:113-127.

KOSSACK, CHARLES W. 1952. A method for autopsying a mourning dove kill. J. Wildl. Mgmt., 16:108.

MCCABE, T. T. 1943. An aspect of collectors' technique. Auk, 60:550-558.

MCCLURE, H. ELLIOTT. 1943. Ecology and management of the mourning dove, *Zenaidura macroura* (Linn.), in Cass County, Iowa. Iowa Agric. Exp. Sta. Res. Bull. 310:353-415.

ODUM, EUGENE P., AND JESSE D. PERKINSON, JR. 1951. Relation of lipid metabolism to migration in birds: seasonal variations in body lipids of the migratory white-throated sparrow. Physiol. Zool., 24:216-230.

RICHDALE, L. E. 1947. Seasonal fluctuations in weights of penguins and petrels. Wilson Bull., 59:160-171.

RIDDLE, OSCAR, AND PELA FAY BRAUCHER. 1934. Studies on the physiology of reproduction in birds. Amer. J. Physiol., 107:343-347.

SMITH, R. S., E. E. DETURK, F. C. BAUER, AND L. H. SMITH. 1924a. Hancock County soils. Ill. Agric. Exp. Sta. Soils Rept. 27. 62pp.

———. 1924b. Mason County soils. Ill. Agric. Exp. Sta. Soils Rept. 28. 62pp.

STURKIE, PAUL D. 1954. Avian physiology. Comstock Publishing Associates, Cornell Univ. Press, Ithaca, N.Y. 423pp.

TABER, WILLIAM BREWSTER, JR. 1930. The fall migration of mourning doves. Wilson Bull., 42:17-28.

WASCHER, H. L., AND R. T. ODELL. 1951. Soils of Cook County. Their properties, productivity and management. Ill. Agric. Exp. Sta. Dept. Agronomy. AG. 1494. 23pp. mimeographed.

WOLFSON, ALBERT. 1942. Regulation of spring migration in juncos. Condor, 44:237–263.

———. 1945. The role of the pituitary, fat deposition, and body weight in bird migration. Condor, 47:95-127.

———. 1954. Weight and fat deposition in relation to spring migration in transient white-throated sparrows. Auk, 71:413-434.

Received for publication October 18, 1956.

CONCLUSIONS FROM A TEN-YEAR CREEL CENSUS ON A LAKE WITH NO ANGLING RESTRICTIONS

Warren Churchill

Wisconsin Conservation Department, Woodruff

The last 15 years have seen drastic changes in the attitude of those responsible for fish management toward fishing regulations. During this period, restrictions on the capture of pan fish have been greatly relaxed or abolished altogether in many states. In the case of game fish, liberalization has been much slower. Ohio has successfully abandoned most restrictions on hook-and-line fishing, and a few other states have liberalized their regulations, but most states are still moving cautiously, if at all, in this direction.

In 1946, Wisconsin established an experimental area to study the effect of liberalized fishing on both game and pan fish (Waggoner and Oehmcke, 1949). Escanaba Lake is one of five lakes included in this area. These lakes were selected because they are typical of the different types of lakes found in northeastern Wisconsin and because their location favors control of anglers by a permit system.

There are no restrictions on hook-and-line fishing for any species of fish. The angler is allowed to keep everything he can catch. A compulsory permit system, similar to that used by Bennett (1954) and Starrett and McNeil (1952) is in effect. Each fisherman is required to obtain a permit, which is issued free at a checking station located at the only landing on the lake. He is also required to return the permit at the conclusion of fishing, and to exhibit his catch to an attendant at the station. In this way, a complete record of the harvest is kept, and other information is collected as desired.

Until 1953, permits for ice fishing were issued and returned at the Trout Lake Forestry Headquarters, about 3 miles from the lake. During evenings and on holidays no one was on duty; and as anglers were required to report their own fish, it is possible that some catches were not recorded. The error thus introduced is probably small. Reported ice fishing for this period constituted 7 per cent of total reported fishing effort and accounted for about 5 per cent of the total walleye catch and 26 per cent of the perch. Failure to report by, for example, 20 per cent of the ice fishermen, would result in errors of about 1 and 5 per cent, respectively, in the total harvest of walleye and perch.

Escanaba Lake is one of the better fishing lakes in northeastern Wisconsin. It covers an area of 293 acres and has a maximum depth of 25 feet. Shore line and bottom contour are irregular, and there are several small islands with rocky bars and shoals. An inlet and outlet are present at high-water stages, but free migration of fish is seldom possible. The water has a total alkalinity of about 25 p.p.m. and is fairly fertile for this area, developing a plankton bloom every summer. Submerged and emergent vegetation is moderately abundant.

The game fish species found in abundance include yellow walleye (*Stizostedion vitreum vitreum*), muskellunge (*Esox masquinongy*), smallmouth bass (*Micropterus dolomieui*), largemouth bass (*M. salmoides*), yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*), bluegill (*Lepomis macrochirus*), and pumpkinseed (*L. gibbosus*). In addition, black crappies (*Pomoxis nigromaculatus*) are present in fairly large numbers but are poorly represented in the anglers' catches. Black bullheads (*Ictalurus melas*) and northern pike (*Esox lucius*) are caught occasionally. White suckers (*Catostomus commersonni*) are abundant. Yellow walleyes are not native to Escanaba Lake. They were introduced by stocking of fry prior to 1940. There has been no further stocking in this lake at any time except for an experimental plant of marked walleye fingerling in 1954.

The Harvest

For the purpose of this report, a fishing year is considered to begin with the disappearance of the ice cover, usually between April 15 and 30. Each year consists of a season of open-water fishing, and the ice-

TABLE 1. — THE ANGLERS' HARVEST FOR THE PERIOD 1946 TO 1955 INCLUSIVE

Fishing Year	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	Annual Average
Total hours fished	9,386	6,295	12,776	19,332	35,862	21,874	25,702	28,862	17,965	23,403	20,146
Hours per acre	32.2	21.6	43.9	66.4	123.2	75.2	88.3	99.1	61.3	79.9	68.7
Total fish caught	9,980	7,058	14,049	10,225	7,871	3,740	5,251	8,186	6,409	24,627	9,740
Fish per acre	34.3	24.3	48.3	35.1	27.0	12.9	18.0	28.1	21.9	84.1	33.2
Total pounds	3,362	2,624	5,765	5,048	7,821	3,487	5,079	5,037	3,133	8,058	4,941
Pounds per acre	11.6	9.0	19.8	17.2	26.7	11.9	17.3	17.2	10.7	27.5	16.9
Fish per hour	1.06	1.12	1.10	0.53	0.22	0.17	0.20	0.28	0.36	1.05	0.48
Pounds per hour	0.34	0.42	0.45	0.26	0.20	0.16	0.20	0.17	0.17	0.34	0.24

fishing season immediately following.

In ten years, 97,396 fish, weighing 49,414 pounds have been taken from Escanaba Lake by anglers (Table 1). Perch made up 46 per cent of the total number and 28 per cent of the total weight. Walleye made up 32 per cent of the number and 55 per cent of the weight. The proportions of perch and walleye in the catch have fluctuated over a wide range (Table 2). In the first two years (1946-47) very few walleyes were taken. In 1948 there was a large catch of walleyes, mostly of the 1947 year class. Since then, this has been the most important species by weight, although not always by number (Klingbiel, 1953). The catch of perch was very high in the first four years. It declined over a three-year period to a minimum in 1952, then increased again to about its original level in 1955.

Annual fluctuations in the species composition of the harvest have been reported from a number of lakes where a creel census has been continued for several years. They were found in Illinois by Starrett and McNeil (1952), in Michigan by Eschmeyer (1939), in Missouri by Kathrein (1953), in Ohio by Pelton (1950), and in Oklahoma by Thompson and Hutson (1951). Such changes are commonly attributed to corres-

TABLE 2. — THE YIELD BY SPECIES FOR THE PERIOD 1946 TO 1955 INCLUSIVE

Fishing year		1946	1947	1948	1949	1950	1951	1952	1953	1954	1955
Yellow walleye	Number	4	47	4,313	2,199	5,887	2,243	3,791	4,683	2,292	5,227[1]
	Pounds	12	59	2,179	2,370	6,720	2,732	4,189	3,740	1,714	3,342
Yellow perch	Number	8,803	6,121	9,026	7,028	1,147	753	393	728	2,072	9,006
	Pounds	2,592	1,958	3,121	2,097	409	349	190	340	488	2,256
Smallmouth bass	Number	635	421	385	540	191	57	156	636	447	329
	Pounds	314	278	264	185	116	61	113	225	207	164
Largemouth bass	Number	167	52	53	62	49	21	90	47	68	146
	Pounds	205	84	65	183	121	46	118	61	64	106
Rock bass	Number	240	306	224	235	380	343	366	1,563	986	1,191
	Pounds	66	122	70	67	108	109	121	406	343	418
Muskellunge	Number	14	7	5	11	34	21	52	20	14	7
	Pounds	91	68	38	74	257	85	200	133	117	32
Other species	Number	117	104	43	150	183	302	403	507	530	8,721
	Pounds	82	55	28	72	90	105	148	132	200	1,740

[1]Includes 1,754 walleye stocked as fingerling in 1954

ponding changes in population density resulting from unequal year classes. Thompson (1941) describes a situation where a large year class of crappies established a cycle of abundance and imposed it on other species. In Escanaba Lake, the sudden increase in the walleye catch in 1948 can be traced directly to a single large year class hatched in 1947. On the other hand, subsequent fluctuations in the size of the annual walleye harvest were not associated with the appearance of large year classes and could hardly reflect changes in population density. The decline and rise of the perch harvest may have been due to changes in abundance, but there is no evidence on this point. Manges (1951) has shown that the species composition of the catch may be affected more by fishing techniques than by relative abundance.

Fishing success has varied from 1.1 fish per hour in the first three years to a low of 0.17 fish per hour in 1951 and back to 1.0 in 1955. These fluctuations follow the catches of pan fish, especially perch, and are related to changes in species composition rather than to productivity. The catch in terms of pounds per hour of fishing has been less variable, ranging from 0.16 to 0.45.

News spreads rapidly among the fishing fraternity, and anglers tend to go where the fish are biting. In a region where good fishing lakes are numerous, fishing pressure on any lake is a reflection of the anglers' estimate of fishing quality. In the case of Escanaba Lake, this estimate seems to be concerned only with walleyes. The large perch catches of the early years attracted only moderate fishing pressure. The appearance of a new walleye population brought on a great increase in fishing from 1948 to 1950, although the quality of fishing as described by the number of fish caught per hour declined steadily during this period (Table 1).

This preference for walleyes is clearly illustrated by a comparison of summer and winter fishing in the fishing years 1954 and 1955. Summer fishing for walleyes was relatively poor in both years. In 1955, record catches of perch and pumpkinseed raised the over-all fishing success to 1.36 fish per hour. This all-time high for summer fishing success did not lead to any increase in fishing pressure so long as walleye fishing did not improve. But when the walleyes started to bite in the winter of 1955-56, word spread rapidly, and ice-fishing pressure for this year was more than twice that of any previous year. Over-all fishing success was only slightly greater than in the winter before (Table 3). The attraction lay in the fact that these fish were walleyes, even though almost half of them were two-year fish averaging about 10 inches in length.

Winter fishing yielded only perch and walleyes in significant numbers. In the first

TABLE 3. — COMPARISON OF SUMMER AND WINTER FISHING FOR THE YEARS 1946-55 INCLUSIVE

	Hours of Fishing		Total Catch of Walleyes		Total Catch of Perch		Total Catch of Other Species		Fish per Hour (All Species)	
Year	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
1946	6,254	3,132	2	2	3,449	5,354	1,170	3	0.74	1.71
1947	5,677	618	38	9	5,287	834	888	2	1.09	1.37
1948	9,403	3,373	4,003	310	4,229	4,797	691	19	0.95	1.52
1949	17,562	1,770	1,930	269	6,256	772	995	3	0.52	0.59
1950	35,166	696	5,716	171	1,140	7	837	0	0.22	0.26
1951	19,740	2,134	1,867	376	644	109	735	9	0.16	0.23
1952	23,483	2,219	3,350	441	373	20	1,062	5	0.20	0.21
1953	25,255	3,607	3,783	900	705	23	2,764	9	0.29	0.26
1954	15,495	2,470	1,938	354	1,421	651	2,029	16	0.35	0.41
1955	15,348	8,055	1,747	3,480	8,791	215	10,364	30	1.36	0.46
Totals	173,383	28,254	24,374	6,312	32,295	12,782	21,535	96	0.45	0.68

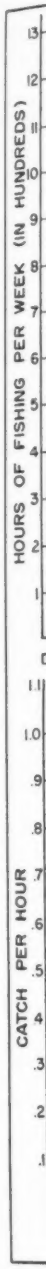


FIG. the c divid been

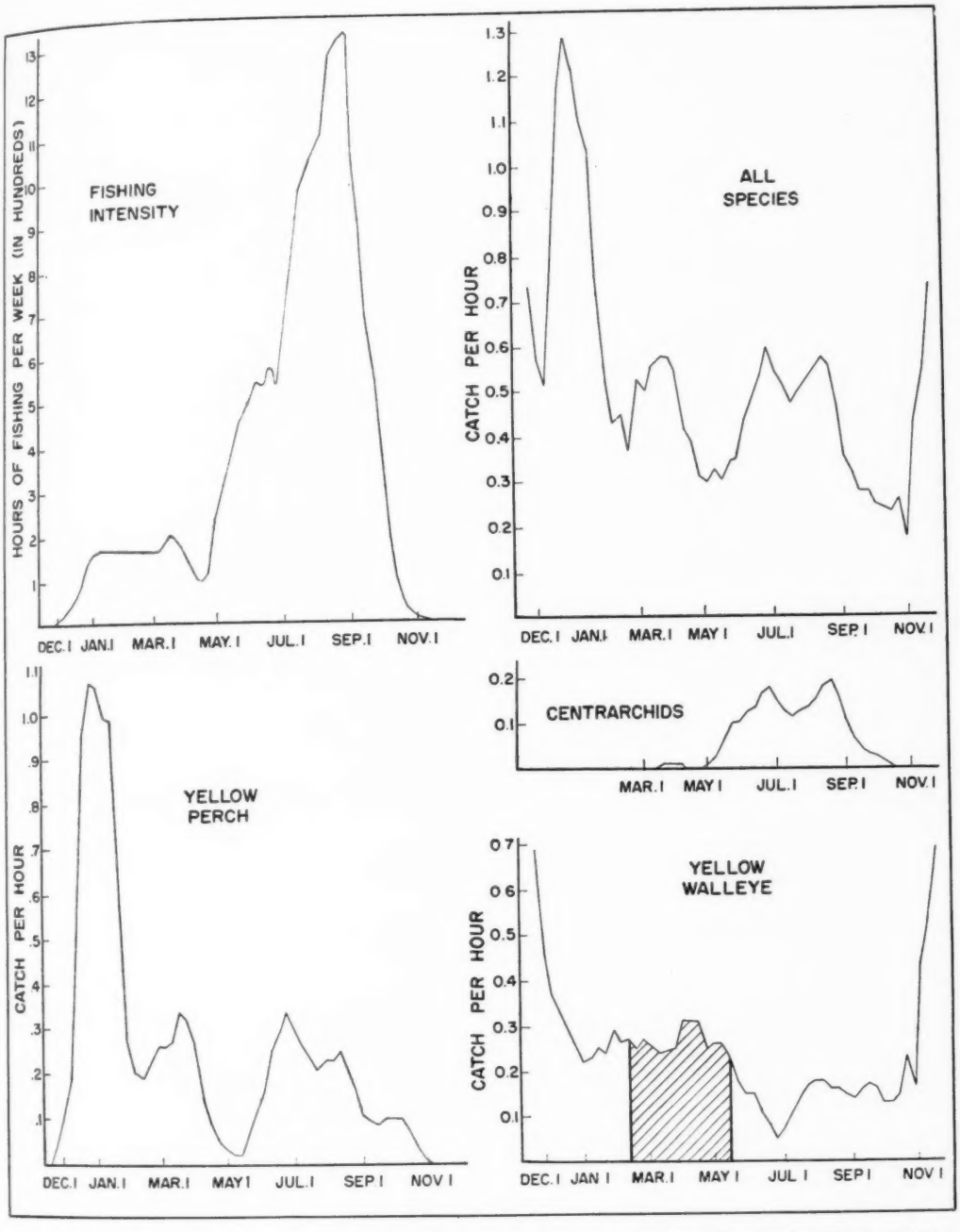

FISHING INTENSITY
HOURS OF FISHING PER WEEK (IN HUNDREDS)
DEC.1 JAN.1 MAR.1 MAY.1 JUL.1 SEP.1 NOV.1
ALL SPECIES
CATCH PER HOUR
DEC.1 JAN.1 MAR.1 MAY 1 JUL.1 SEP.1 NOV.1
CENTRARCHIDS
MAR.1 MAY 1 JUL.1 SEP.1 NOV.1
YELLOW PERCH
CATCH PER HOUR
DEC.1 JAN.1 MAR.1 MAY1 JUL.1 SEP.1 NOV 1
YELLOW WALLEYE
CATCH PER HOUR
DEC.1 JAN 1 MAR.1 MAY 1 JUL 1 SEP.1 NOV 1

FIG. 1. Seasonal variation in fishing intensity and fishing success calculated by weeks. Each point on the curves for fishing success represents the total number of fish caught in the same week for ten years divided by the total number of hours of fishing effort in the same week for ten years. All curves have been smoothed by a moving average of 3. The shaded area in the walleye curve represents the closed season on walleye in northern Wisconsin.

TABLE 4. — FISHING REGULATIONS IN WISCONSIN 1946-53

Species	Closed Season	Minimum Size	Daily Bag Limit
Yellow walleye	Jan. 16-May 15	13 in.	5[1]
Large and smallmouth bass	Jan. 16-June 19	10 in.	5[1]
Muskellunge	Nov. 2[2]-May 24	30 in.	1
Pan fish: 1946-49	Jan. 16-Apr.20	none	25 each species[3]
Pan fish: 1950-53	none[4]	none	25 each species

[1]Bag limit of 7, 1946-48
[2]Jan. 16 in 1946-48
[3]No bag limit on perch 1946-49
[4]Closed season March 16 to April 28, 1950

three years, when the yellow perch was the dominant species, fishing success was noticeably higher in winter than in summer. In subsequent years, success was more uniform and in 1955 for the first time, summer fishing was more successful than winter, due to large summer catches of perch and centrarchids, followed by a very low winter perch harvest. The year 1955 was also the first period in which the winter catch of walleyes exceeded or even approached that of the preceding summer. It must be noted that 40 per cent of the winter catch was composed of fish stocked in 1954, but even the catch of native walleyes exceeded the summer total. This increased winter catch of native walleyes was composed of individuals from several year classes that were available to anglers the previous summer. It was not the result of the entrance of a strong year class into the fishery. Similarly, the low winter catch of perch was not due to a low population, since large catches were made in both the preceding and following summers. The reason for the apparent change in habits of the two species is not known.

Since Escanaba Lake is located in vacation country with a small permanent human population, summer fishing pressure is always much higher than winter, regardless of relative success (Fig. 1). The lower success rate in summer may be due, in part, to the large proportion of inexperienced fishermen. Winter anglers are mostly natives familiar with the lake. However, there are certain seasonal fluctuations in the success that can be attributed to varying vulnerability of one or two species. The most noticeable of these fluctuations is a brief period of very high success for perch in early winter. This is apparent even in years when the total perch catch is low. Both perch and walleye have a short season of low vulnerability in early summer, but the periods for the two species do not coincide. The records also seem to show a short and sudden increase in vulnerability of walleye in late fall. However, fishing pressure at this time is so low that the validity of this feature must be questioned.

The factors responsible for seasonal changes in the catchability of fish are not known. Christensen (1953), studying 11 lakes in Michigan with apparently similar populations, found that fishing success was higher in winter on some lakes and higher in summer on others. Moyle and Franklin (1953, 1954, 1955) found similar disagreement in a series of lakes in Minnesota. Hazzard and Eschmeyer (1937) reported that the catch per hour was much lower in winter than in summer on Michigan lakes where intensive creel censuses were conducted. The general creel census for the same year showed almost equal rates of success for summer and winter fishing in the entire state.

EFFECT OF REGULATIONS

The harvest discussed above was taken in the absence of restrictions on hook-and-line fishing. If the regulations that were in effect throughout the state during these years (Table 4) had been in force on Escanaba Lake, the catch of game fish would have been reduced by well over 50 per cent.

Analysis of the unrestricted catch shows that the effect of regulations is quite similar on the catch of both yellow walleye and smallmouth bass. Table 5 shows the reduction in the harvest that would have been brought about by each of these regulations in terms of percentage of the actual catch. Of the three restrictions considered here, the size limit has the greatest effect on the number of fish taken, reducing the catch

TABLE 5. — ESTIMATED EFFECT OF ASSUMED REGULATIONS ON THE CATCH OF YELLOW WALLEYE AND SMALLMOUTH BASS 1947-53 INCLUSIVE

Assumed regulations	Estimated Percentage Reduction from Actual Catch[1]			
	Walleye		Smallmouth Bass	
	Number	Weight	Number	Weight
Bag limit only	13	9	8	6
Closed season only	16	18	6	7
Minimum-size limit	39	18	61	31
Closed season and bag limit	27	25	14	12
Minimum size and bag limits	42	23	62	33
Minimum size and closed season	51	34	64	36
Minimum size, bag limit, and closed season	54	37	65	39

[1]The actual catch with no restrictions was 23,116 walleye weighing 21,930 pounds and 3,021 smallmouth weighing 1,556 pounds.

by more than the bag and season limits combined. The reduction of the catch by combined restrictions on size and bag limits is only slightly greater than that effected by the size limit alone, since most large catches of walleyes and smallmouth bass were made up of small fish. The effect of the closed season, on the other hand, is largely independent of the other two restrictions. If size limit and closed seasons are in effect, a bag limit affords little additional protection.

The hypothetical effect of regulations on the muskellunge catch is comparable to that on yellow walleye and smallmouth bass. Of 164 muskellunge caught in eight years, 24 (15 per cent) were taken out of season. No size records are available for the 14 taken in 1946, but 102 (68 per cent) of the others were less than the legal length of 30 inches. There is no record of anyone's taking more than one muskellunge in one day, but a combined size limit and closed season would have reduced the catch by 75 per cent.

There is currently no size or season limit on pan fish in Wisconsin, and the bag limit is 25 of each species. Relatively few catches from Escanaba Lake have exceeded this number. A bag limit of 25 on yellow perch would have reduced the catch in the first few years by not more than 10 per cent.

The effect of a minimum-size limit will vary greatly from year to year, depending on the population structure. For example,

TABLE 6. — THE CATCH OF YELLOW WALLEYE AND SMALLMOUTH BASS THAT WOULD HAVE BEEN ILLEGAL UNDER STATE-WIDE REGULATIONS

Fishing year	1947	1948	1949	1950	1951	1952	1953
Yellow walleye							
Total number in catch	—	4,313	2,199	5,887	2,243	3,791	4,683
Per cent of catch							
Under 13 inches long	—	73	31	16	17	32	56
Taken in excess of 5 per person	—	29	9	9	6	7	12
Taken during closed season	—	7	19	3	37	22	22
Smallmouth bass							
Total number in catch	421	385	540	191	57	156	636
Per cent of catch							
Under 10 inches long	37	53	72	33	7	68	84
Taken in excess of 5 per person	0	2	20	0	0	12	10
Taken during closed season	5	5	4	8	9	6	8

the percentage of a year's catch that would have been below legal size elsewhere in Wisconsin varied from 16 to 73 for walleyes and from 7 to 84 for smallmouth bass (Table 6). This percentage is highest in those years in which a large year class is approaching the legal size. Since they consist mostly of small fish, catches in excess of the state-wide limit are highest in the same years.

Because of the seasonal variation in fishing pressure already described, the record of Escanaba Lake cannot be considered to give a complete picture of the effect of the closed season. Fishing success for walleyes during the period of this closed season is greater than at most times in the open season. In addition, fishing pressure on Escanaba Lake at this time is relatively low because of its remote location. If the lake were located near a center of population, it would probably attract heavy fishing pressure, resulting in a large harvest during the elsewhere-closed season.

After ten years of unrestricted fishing, there is no evidence of damage to the fish population of Escanaba Lake (Oehmcke and Waggoner 1956). There have been great variations in the size of the harvest, but no consistent trend that could be interpreted as depletion. Similarly, the changes in species composition have not been consistent enough to suggest any permanent change in the population structure. It is believed that the population can maintain itself indefinitely under existing fishing conditions.

SUMMARY

In Wisconsin, Escanaba Lake has been under experimental management since 1946, with no restrictions on hook-and-line fishing for any species. A complete record of the harvest is kept, and other information is collected by means of a compulsory permit system. In ten years, 97,387 fish weighing 49,414 pounds have been harvested. Perch and walleye together made up about 80 per cent of the catch, but the proportions of the two species in the catch have varied greatly from year to year. Fishing success has varied from 0.17 to 1.1 fish per hour. Fishing restrictions in effect elsewhere in Wisconsin would have reduced the 10-year catch of game fish by more than 50 per cent. Minimum size limits would have had more effect than bag and season limits. There is no evidence of depletion after ten years of unrestricted fishing.

LITERATURE CITED

BENNETT, GEORGE W. 1954. Largemouth bass in Ridge Lake, Coles County, Illinois. Bull. Ill. Nat. Hist. Surv., 26(2):217-276.

CHRISTENSEN, KENNETH E. 1953. Fishing in twelve Michigan lakes under experimental regulations. Mich. Dept. Cons., Inst. for Fisheries Res. Misc. Pub. No. 7:1-46.

ESCHMEYER, R. WILLIAM. 1939. Summary of a four-year creel census on Fife Lake, Michigan. Trans. Amer. Fish. Soc., 68:354-358.

HAZZARD, A. S., AND R. W. ESCHMEYER. 1937. A comparison of summer and winter fishing in Michigan lakes. Trans. Amer. Fish. Soc., 66: 87-97.

KATHREIN, JOSEPH W. 1953. An intensive creel census on Clearwater Lake, Missouri, during its first four years of impoundment, 1949-1952. Trans. N. Amer. Wildl. Conf., 18:282-295.

KLINGBIEL, JOHN. 1953. Are fishing restrictions necessary? Wis. Cons. Bull., 18(11):3-5.

MANGES, DANIEL E. 1951. Is there a harvestability differential in fish? Trans. Amer. Fish. Soc., 80:46-49.

MOYLE, JOHN B., AND DONALD R. FRANKLIN. 1953. Creel census of 23 Minnesota lakes—1952. Minn. Dept. Cons., Fish. Res. Invest. Rept., 135:1-71 (mimeo.).

———. 1954. Creel census of 12 Minnesota lakes December 1, 1952 to December 1, 1953. Minn. Dept. Cons., Fish. Res. Invest. Rept., 146: 1-36 (mimeo.).

———. 1955. Creel census of 12 Minnesota lakes December 1, 1953 to December 1, 1954. Minn. Dept. Cons., Fish. Res. Invest. Rept., 159: 1-35 (mimeo.).

OEHMCKE, ARTHUR A., AND D. W. WAGGONER. 1956. How liberal can you get? Wis. Cons. Bull., 21(5):12-15.

PELTON, JOHN Z. 1950. Three years of liberalized fishing at Lake Alma, Ohio. Trans. Amer. Fish. Soc., 78:64-69.

STARRETT, WILLIAM C., AND PERL L. MCNEIL, JR. 1952. Sport fishing at Lake Chautauqua, near Havana, Illinois in 1950 and 1951. Ill. Nat. Hist. Surv., Biology Notes, 30:1-31.

THOMPSON, DAVID H. 1941. The fish production of inland streams and lakes. Pp. 206-217 *in* A symposium on hydrobiology. Univ. Wis. Press, Madison. 405pp.

THOMPSON, WILLIAM H., AND DON HUTSON. 1951. A ten-year creel census on Lake Pawhuska, Oklahoma. Trans. Amer. Fish. Soc., 80:11-27.

WAGGONER, D. W., AND A. A. OEHMCKE. 1949. Come and get 'em! Wis. Cons. Bull., 14(5): 3-6.

Received for publication October 8, 1956.

MULE DEER AND ELK FOOD HABITS ON THE NATIONAL BISON RANGE[1]

Melvin S. Morris and John E. Schwartz

Montana State University, Missoula, and U.S. Fish and Wildlife Service, Moiese, Montana

The reduction program of surplus elk and mule deer on the National Bison Range in western Montana in 1951 and 1952 provided an opportunity to determine the relative food habits of these two game species (*Cervus canadensis* and *Odocoileus hemionus*) on a range that is predominantly grassland.

The Pauline pasture was selected as a source of animals. It is 5,566 acres in size. It contains the principal forage species and plant-cover types of the Bison Range and is accessible throughout the year. Fig. 1 illustrates the extent and distribution of the main cover types. The grassland consists largely of Palouse Prairie vegetation, with bluebunch wheatgrass (*Agropyron spicatum*) as the principal species. The forested portion of the pasture is predominantly Douglas-fir (*Pseudotsuga menziesii* [*P. taxifolia*]) on northern exposures and ponderosa pine (*Pinus ponderosa*) on the southern exposures. Swales and drainage courses contain snowberry (*Symphoricarpos occidentalis*) and hawthorn (*Crataegus douglasii*). Rocky outcrops and stony areas give rise to scattered stands of chokecherry (*Prunus demissa*), serviceberry (*Amelanchier alnifolia*), and mockorange (*Philadelphus lewisii*). Rocky Mountain maple (*Acer glabrum*) is commonly found as an understory species in the forest type. Ninebark (*Physocarpus malvaceus*) is abundant at the margins of the Douglas-fir type. Fig. 2 shows the arrangement of types relative to the topography of the pasture.

Methods and Results

Data were secured on the botanical characteristics of the range, plant development, snow conditions, and other meteorological information, in addition to the stomach samples of deer and elk. The study extended over the period from November 1951 to mid-November 1952.

Data on the botanical characteristics of the food supply were secured by determining the density and percentage of composition on sample plots, each containing 100 square feet and located at two-chain intervals along traverse lines through each subtype. These data were weighted by type acreage, aggregated for the pasture as a whole and were then converted to a weighted percentage of

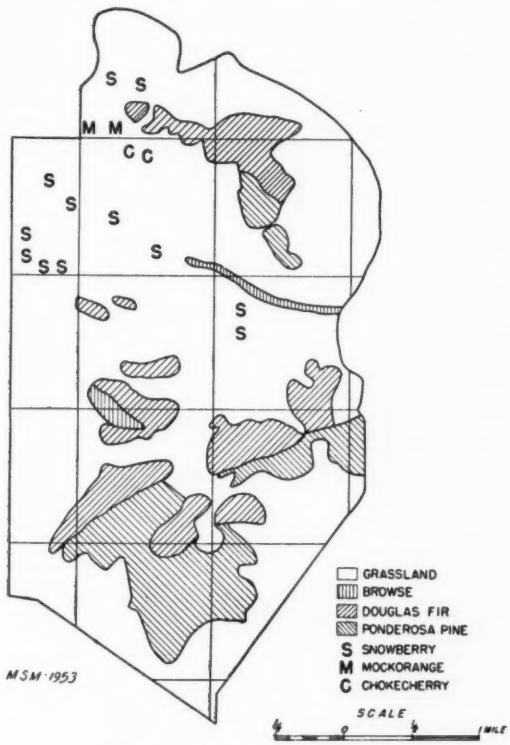


Fig. 1. Plant cover types in the Pauline pasture study area showing amount and distribution of major forage types.

[1] Contribution from the Montana Cooperative Wildlife Research Unit; U.S. Fish and Wildlife Service, Montana State Fish and Game Department, Montana State University, and Wildlife Management Institute cooperating.

FIG. 2. View of Pauline pasture. Palouse Prairie and Montane Forest are the principal vegetation zones of the study area.

the vegetation of the entire pasture. While this does not represent the relative volumes of herbage contributed by each species to the available forage supply, it is indicative of the character of the food available. This information is contained in Table 1. Grasses make up approximately 79 per cent of the botanical composition of the vegetation, while herbs and shrubs make up 7 and 14 per cent, respectively.

Weather records were secured from the station located at the range headquarters, which is near the north end of Pauline pasture. Observations on snow conditions and

TABLE 1. — BOTANICAL COMPOSITION OF THE VEGETATION IN PAULINE PASTURE, NATIONAL BISON RANGE

Grasses	Per cent	Forbs	Per cent	Shrubs	Per cent
Agropyron spicatum	27.6	*Balsamorhiza sagittata*	3.4	*Philadelphus lewisii*	2.6
Bromus tectorum	12.0	*Achillea lanulosa*[1]	1.1	*Acer glabrum*	2.3
Festuca idahoensis	9.6	*Pentstemon* sp.	0.9	*Artemisia frigida*	1.7
Poa secunda	9.0	*Lupinus* sp.	0.7	*Amelanchier alnifolia*	1.5
Aristida longiseta	4.9	*Aster* sp.	0.7	*Physocarpus malvaceus*	1.3
Festuca scabrella	4.8	*Arnica* sp.	Tr.	*Artemisia dracunculus*	1.2
Calamagrostis rubescens	4.3			*Prunus demissa*	1.1
Koeleria cristata	3.6			*Ribes cereum*	1.1
Poa pratensis	2.7			*Arctostaphylos uva-ursi*	1.1
Stipa comata	0.4			*Symphoricarpos occidentalis*	0.4
Elymus cinereus	Tr.				
Total	78.9	Total	6.8	Total	14.3

[1] Same as *Achillea millefolium* ssp. *lanulosa*

TABLE 2.—ENVIRONMENTAL CONDITIONS ON NATIONAL BISON RANGE THROUGH PERIOD OF STUDY, NOVEMBER 1951–NOVEMBER 1952

Month	Meteorological Data					Condition and Availability of Forage at the Time of Sampling	
	Precip. (In.)	Snow-fall (In.)	Temperature (°F.) Mean Max.	Mean Min.	Average		
Nov.	0.42	4.0	43	23	33	Nov. 9.	Herbage mature, some green cheatgrass, all forage available. No snow.
Dec.	1.32	25.0	31	13	22		
Jan.	0.42	7.5	30	9	20	Jan. 1.	Grasses and some herbs available along edges of surface rock. Deep snow, crusted.
Feb.	0.45	8.0	40	18	29	Feb. 8.	Bluebunch wheatgrass with 1-3 inches of green growth at base of plants. Cheatgrass green. South slopes open. Open spots on north shopes.
Mar.	0.25	3.0	47	23	35	Mar. 7.	Herbage as above. All southerly exposures open. Open spots on north slopes.
Apr.	0.03	—	67	29	48	Apr. 4.	Shrubs budded out. Grasses show 2-5 inches of new growth. Balsamroot leaves up 3 inches. Snow gone except under trees.
May	1.86	—	69	41	55	May 5.	Currants in full bloom, mockorange leafed out. Balsamroot in full bloom. Sandberg bluegrass headed out on south slopes.
June	2.45	—	78	45	55	June 6.	Balsamroot through blooming. Cheatgrass red on south slopes. Bluebunch wheatgrass headed out.
July	0.18	—	85	46	66	July 3.	Seed heads mature on bluebunch wheatgrass, leaves green.
Aug.	0.53	—	85	47	66	Aug. 29.	Bluebunch wheatgrass stems and leaves brown on south slopes. Shrubs with green leaves.
Sept.	0.52	—	79	41	61		
Oct.	0.07	—	67	27	47	Oct. 3.	No fall green up of grass. Leaves still on shrubs.
Nov.	0.60	0.8	44	21	33	Nov. 14.	No green feed on grasses or forbs. Leaves mostly gone from shrubs.

herbage development and condition were obtained on most of the dates when stomach samples were secured. Snow depth, snow crust, and greenness of herbage were considered as possible contributing factors affecting forage use. Table 2 contains a summary of this information. For the most part, meteorological conditions were normal for the period of the study. The following observations are considered to be significant. There was a fall "green up" of grasses in 1951, but not in 1952. Snow in December was such as to make much of the low herbage less available to animals. The lowest temperatures were recorded during January and December. Sampling on January 1 was undertaken on one of the coldest days of the year.

Analysis of stomach samples was used as the sole means of determining the use of herbage, as the range was used concurrently by deer, elk, and bison (*Bison bison*), and all three were found feeding in all the cover types. Stomach samples were taken at approximately monthly intervals from November 1951, to November 1952. However, the first samples from elk were not taken until December. Four deer and two elk were taken each month. A period of 57 days intervened between the July 3 and August 29 sampling. No samples were taken in September. The July 3 sample consisted of only

two deer and one elk. For comparison, additional samples of elk were obtained by the Montana Fish and Game Department, two from the upper Blackfoot Valley and two from the Sun River elk winter range. These were secured on the same date as the last sampling on the Bison Range. All samples were treated with a 10 per cent formalin solution and then washed in fine-mesh bags. They were stored until the end of the sampling period. The volumetric-percentage analysis of the samples was carried out by Howard Leach and C. M. Ferrel in the laboratory of the California Game and Fish Department.

In Table 3, the data represent the average of the samples for each collecting date. The volumetric percentage for each forage class varied more for deer from month to month than it did for elk. The elk samples were uniform in the amount of grass contained from month to month. The August elk samples contained a considerable amount of forbs and somewhat significant amounts in June and July.

The deer samples exhibit some interesting characteristics. One usually expects to find considerable grass in the diet of deer in the spring months (Dasmann, 1949). Our data indicate that the November and December consumption of grass was also high, while unexpectedly low for shrubs. Conifers made up the principal food element of the January deer samples, being 74 per cent of the volume. Deciduous shrubs usually are considered to be characteristic of mule deer diets, and in the samples taken, shrubs made up a sizable portion of the volume. This was particularly true of the August 3 data when the shrub class averaged 60 per cent of the volume.

While the data presented are grouped into grasses, forbs, shrubs, and conifers, the original records indicate some selectivity of species. Balsamroot (*Balsamorhiza sagittata*) appears in individual deer samples at all periods of the year. One deer stomach sample on June 6 contained 35 per cent balsamroot. Bull-thistle (*Cirsium* sp.) was found in several samples and made up 65 per cent of the volume of a deer sample on November 11. Fringed sagebrush (*Artemisia frigida*), a common evergreen half-shrub found at lower elevations and on some southern exposures, made up 10 per cent of the volume in one November and one February sample. Golden aster (*Chrysopsis villosa*), while not of sufficient abundance to make up a significant portion of the plot data, was used heavily. It appeared in the deer samples of August, October, and November. One August sample was 90 per cent golden aster; an October sample, 92.

Snowberry and chokecherry were the two principal deciduous shrubs found in the samples. They were abundant in the spring and summer samples. A deer sample in May contained 40 per cent chokecherry. In one August deer sample, 90 per cent was snowberry. Leaves appeared to be the main portion of the plant taken. Very little pine was found in the samples. Douglas-fir appeared in the December, January, and February samples. As Table 3 shows, conifers made up 74.2 per cent of the volume in January and this was exclusively Douglas-fir. The

TABLE 3. — HERBAGE COMPOSITION OF MULE DEER AND ELK STOMACH SAMPLES EXPRESSED AS VOLUME PERCENTAGES, NOV. 9, 1951–NOV. 14, 1952

Dates Sampled . . .	Nov. 9	Dec. 6	Jan. 1	Feb. 8	Mar. 7	Apr. 4	May 5	June 6	July 3	Aug. 29	Oct. 3	Nov. 14
DEER												
Grasses	56.5	74.2	1.3	86.0	97.7	84.0	11.3	5.0	Tr.	Tr.	Tr.	Tr.
Forbs	41.0	24.2	24.5	10.2	2.3	16.0	71.2	73.2	72.5	40.0	93.0	100.0
Shrubs	2.5	0.3	Tr.	2.5	Tr.	Tr.	17.5	21.8	27.5	60.0	7.0	Tr.
Conifers	—	1.3	74.2	1.3	—	—	—	—	—	—	—	—
ELK												
Grasses	—	99.5	100.0	100.0	100.0	100.0	99.5	96.5	90.0	67.5	100.0	100.0
Forbs	—	—	Tr.	Tr.	Tr.	Tr.	0.5	3.5	10.0	32.5	Tr.	Tr.
Shrubs	—	0.5	Tr.	—	—	—	Tr.	Tr.	—	Tr.	Tr.	Tr.
Conifers	—	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	Tr.	—	—

limited purpose of the study precluded the need for detailed separation of grasses by species in both the elk and deer samples.

DISCUSSION

Any attempt to interpret the significance of the botanical characteristics of the stomach samples must be largely conjectural. The large percentage of grass in the samples of both deer and elk suggests either a high preference for grass or a limited supply of more desirable forage. In the case of elk, it is perhaps a matter of preference. Reports of studies elsewhere indicate that elk may make considerable use of grass (De Nio, 1938). Our range survey (Table 1) and the heavily browsed condition of this class of forage particularly on chokecherry, serviceberry, and mockorange, do imply that shrubs were in limited supply.

The limited supply of browse, maturity of forbs, and the green fall growth of grass in November 1951 may partly explain the high percentage values of grass in the deer samples of that time. The lack of fall growth of grass in 1952 and the low percentage of grass in the deer samples of October and November appear to be consistent with the previous interpretation. The presence of forbs in large amounts through the year would indicate a high degree of substitution of this class of forage for shrubs on this type of range. This phenomenon is somewhat similar to the food habits exhibited by pronghorn antelope (*Antilocarpa americana*) in Texas on a range low in shrubby vegetation (Buechner, 1950). The use of golden aster in large amounts in the late summer and fall diet of deer suggests either an abnormal palatability in this species or substitution for browse. The presence of a high percentage of Douglas-fir in the January 1 samples of deer is difficult to interpret. Temperature, snow condition, or wind breakage of fir are all possible factors. It has been observed by the authors that deer may make heavy use of Douglas-fir in November if it is made accessible by wind breakage of trees or by logging. In this case, the low temperatures and deep snow may have caused the deer to yard up on north-facing slopes in young stands of Douglas-fir with resulting heavy use of fir.

The food habits of deer on this type of range appear to be more closely related to those of the mule deer of California (Dasmann, 1949; Dixon, 1934) and southeastern Washington (Buechner, 1952) than to the deer of Utah (Julander, 1955) insofar as the use of grass is concerned.

SUMMARY

The relative food habits of mule deer and elk were studied on a game range that consists mainly of grassland and forest with a grass understory.

Weather records indicated a fairly normal period for the study except for an unusually dry fall in 1952 which limited fall growth of grasses and forbs. Snow and the low winter temperatures were important factors in conditioning the availability and use of forage in the winter. Grasses were the principal forage material in the yearlong diet of the elk. Mule deer made unexpected use of grass as indicated by the November and December 1951 samples. The degree of use of grass in the spring was as anticipated. Forbs were preponderant in the samples from May to November 1952. Douglas-fir was the principal constituent in the January 1 samples.

BIBLIOGRAPHY

BUECHNER, HELMUT K. 1950. Life history, ecology and range use of the pronghorn antelope in Trans-Pecos Texas.. Amer. Midl. Nat., 43:257-354.

———. 1952. Winter-range utilization by elk and mule deer in southeastern Washington. J. Range Mgmt., 5:76-80.

DASMANN, W. P. 1949. Deer-livestock forage studies on the interstate winter deer range in California. J. Range Mgmt., 2:206-212.

DE NIO, R. M. 1938. Elk and deer foods and feeding habits. Trans. N. Amer. Wildl. Conf., 3: 421-427.

DIXON, JOSEPH S. 1934. A study of the life history and food habits of mule deer in California. Calif. Fish and Game, 20:181-182, 315-354.

JULANDER, ODELL. 1955. Deer and cattle range relations. Forest Science, 1:130-139.

Received for publication August 16, 1956.

RELATION OF HAY HARVESTING TO DUCK NESTING UNDER A REFUGE-PERMITTEE SYSTEM

Ronald F. Labisky[1]

U.S. Fish and Wildlife Service, Minneapolis; and Department of Forestry and Wildlife Management, University of Wisconsin, Madison

This paper discusses the seriousness of duck-nest destruction caused by haying operations on a waterfowl breeding refuge and suggests some management practices for reducing such losses. While this paper deals specifically with the refuge problem, some of the recommendations may apply to private lands as well, where hayfield duck-nest losses are perhaps of even greater magnitude.

While much has been written concerning hayfield-nest destruction among upland game birds, little research has been published along similar lines among duck species. In order to reduce hayfield-nest destruction, English (1934) advised leaving islands of unmowed hay surrounding pheasant (*Phasianus colchicus*) nests. Bennett (1938) and Bell (1954) afforded similar protection to duck nests. These workers located the nests with the aid of a flushing bar at the time of mowing. The data presented in this paper were collected during the 1954 and 1955 nesting seasons at Horicon National Wildlife Refuge, Mayville, Wisconsin. The refuge consists of 20,683 acres, about 1,500 of which are in upland. This study was conducted on the upland area, much of which is under cultivation. The cultivated acreage is subdivided into 43 farm units, each managed on a share-cropping basis between the refuge and a farmer permittee. Operation of the farm units is based mainly on a five-year rotation plan with a 20-40-40 cropping system—20 per cent grain (generally oats) with a legume-hay seeding, 40 per cent legume hay, and 40 per cent corn. The legume hays are left in rotation for two years.

Since the refuge has no direct use for the hay, except as a green-manure crop, it has been the practice of the permittee to take all of the hay as a part of his crop-division share. The hayfields consist predominantly of alfalfa and red clover, with some timothy. The first year that the hay is in the rotation, the permittee is allowed to harvest a first and second cutting. The second year, the first crop may be cut, but the second crop must be plowed under as green manure. This paper deals only with the first hay cutting.

Haying operations were tractor-powered and consisted of mowing, side-delivery raking, and baling or chopping. The exception to this procedure was direct clipping by a self-propelled hay cutter-chopper. This was used by only one permittee.

The grain and corn are divided on a percentage basis with the permittee. The refuge share of corn is usually left in the field to provide waterfowl food.

Efforts to place more refuge land under cultivation at Horicon may increase the magnitude of hayfield-nest destruction. However, since the completion of this study, the refuge has undertaken limited farming on its own (about 250 acres in 1956), thus greatly reducing possible nest destruction on those acres. The added acreage will provide additional food that will enable the refuge area to hold a larger flight of Canada geese (*Branta canadensis*) during the fall. The fall concentration peak at Horicon in 1954 reached 47,000 Canada geese (Gunther, 1954).

The Nesting Population

Improved marsh habitat resulting from an earthen dike, constructed across the south end of the refuge in 1951, brought an increased number of waterfowl to Horicon during the 1952 nesting season. Although brood counts are not available for 1953, a sizable increase in brood production over that for 1952 was evident. A nonrandom 10-per-cent brood transect of the marsh showed 300 broods in 1954 and 400 in 1955—an increase of 33 per cent. Blue-winged teal (*Anas discors*), mallards (*A. platyrhynchos*), and redheads (*Aythya americana*)

[1] Present address: Illinois Natural History Survey, Urbana, Illinois.

TABLE 1. — TOTAL NUMBER OF DUCK NESTS LOCATED IN 1954 AND 1955

Year	1954			1955			1954-55		
Acres of hay	309			283			592		
Species	No.	Per Cent	Nests/ Acre	No.	Per Cent	Nests/ Acre	No.	Per Cent	Nests/ Acre
Blue-winged Teal	55	56	0.18	82	77	0.29	137	67	0.23
Mallard	44	44	0.14	24	23	0.09	68	33	0.11
Totals	99	100	0.32	106	100	0.38	205	100	0.35

comprised 44 per cent, 34 per cent, and 8 per cent, respectively, of the total brood production for the years 1954 and 1955. With an increase in the breeding population of dabbler species using the marsh, there is an accompanying increase in the potential number of ducks nesting in hayfields. Blue-winged teal and mallards were the only species encountered nesting in the upland hayfields.

There was an increase of 49 per cent in the number of blue-winged teal, and a decrease of 45 per cent in the number of mallards nesting in the legume hayfields in 1955 (Table 1). The nest ratio in hayfields for both 1954 and 1955 approached 2:1, blue-winged teal over mallards.

The 1954-55 nest density for both species combined was approximately one nest per three acres of hay. In certain fields, however, the nesting density reached a figure of 1.8 duck nests per acre.

The two-year average distance of nests from water was 229 yards for 68 mallards and 221 yards for 137 blue-winged teal. There was very little yearly variation. Since these nests were all located in upland hayfields, the mean distances to water are greater than those reported by other workers. On the Ruthven Area in Iowa, Bennett (1938) and Glover (1956) found that blue-winged teal nests averaged 41.5 yards and 79.4 yards from water. In Montana, the average distance of mallard nests from water was 118.7 yards (Girard, 1941). The average distance of nests from the field edge in this study was 24 yards for both species. There was no correlation between the distances of the nests from the field edge or water and their success in hatching.

NEST MORTALITY

The number of waterfowl nests destroyed by haying operations was determined by checking each field after the hay was removed. Destroyed nests were easily located, as broken egg shells, down, or other nest materials were clearly visible against the closely cropped hay.

The hayfields were searched after hay removal by driving a truck through them with an observer seated atop the cab. In some cases, inaccessibility or wet field conditions required that the fields be walked. Not only was walking more time consuming, but it was also less efficient due to the lower position of the observer. Errors might have

TABLE 2. — FATE OF MALLARD AND BLUE-WINGED TEAL NESTS

Years	1954		1955	
Acres of hay	309.0		283.0	
Nest category	No.	Per Cent	No.	Per Cent
Hatched before haying	14	14	23	22
Destroyed by predators before haying	0	0	3	3
Destroyed directly by haying	78	78	32	30
Destroyed indirectly by haying	7	7	5	5
Protected from haying	0	0	43	40
Totals	99	99	106	100

occurred merely by overlooking a nest or because a nest was completely obliterated by haying operations.

The 1954 dates of hay cutting extended from June 12 to July 18; the major period of the hay harvest occurred during late June and early July. In 1955, the majority of the hay was cut about one week earlier than in 1954. The hayfields were generally searched for destroyed nests within one or two days following mowing.

All nests active at the time of mowing were destroyed (Table 2). With the exception of one nest, Bennett (1938) found this to be true of the blue-winged teal in Iowa. In the present study, the majority of the nests were either mowed through or crushed by the tractor tires. Very frequently, the nests not destroyed by mowing were preyed upon soon after by crows (*Corvus brachyrhynchos*) or mammals. If, however, the nests survived mowing and predation, they were destroyed later by raking, baling, or chopping operations.

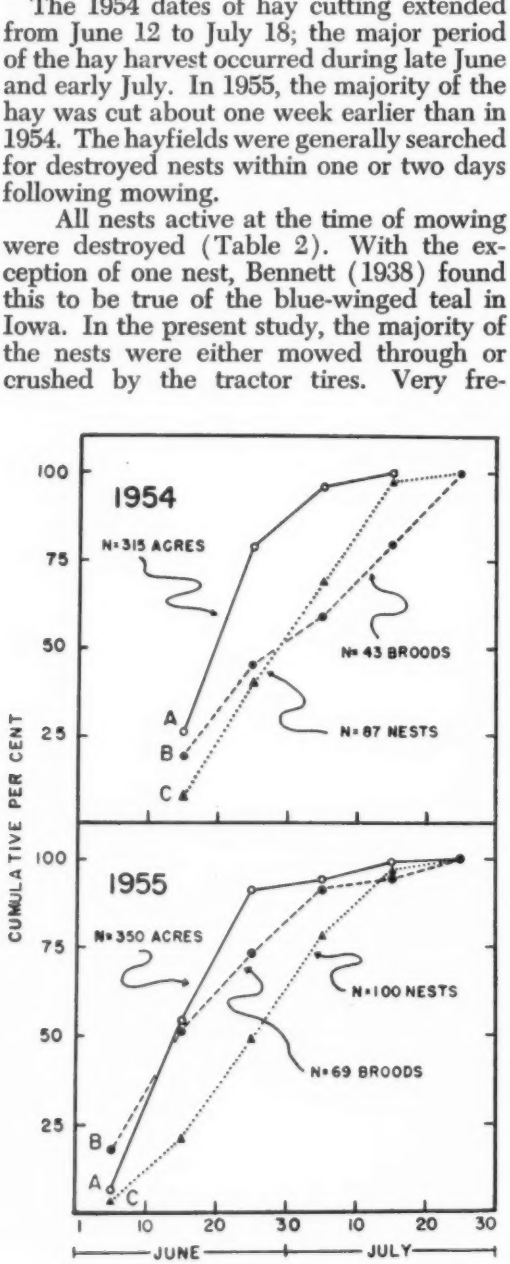


FIG. 1. Cumulative per cent comparison between 1954 and 1955 (A) hayfield mowing, (B) hatching of marsh nests, and (C) potential and actual hatching of hayfield nests; mallard and blue-winged teal data combined.

In 1954 only 14 per cent of the nests hatched before haying, while 22 per cent hatched before haying in 1955 (Table 2). The 1955 hay crop was harvestable on June 1, but heavy rains delayed mowing for about ten days. This delay in mowing allowed more nests to hatch than would have under weather conditions favorable to normal mowing.

The hatching curves for marsh nests, presented in Fig. 1, are the result of backdating to hatching the Class Ia broods (Gollop and Marshall, 1954) observed on the nonrandom 10-per-cent refuge-transect area. Only a small percentage of the hayfield nests hatched before haying, but these data are supplemented by estimating the potential hatching dates of the destroyed nests from their incubation stages at the time of destruction.

The spring of 1955, for both legume vegetation and nesting, was earlier than the 1954 season. The cumulative 50-per-cent points in hayfield mowing occurred on June 25, 1954, and June 20, 1955. The earliness of the 1955 season is further confirmed by the late-June hatching data (Fig. 1), which show (1) a cumulative 9-per-cent increase over 1954 in the potential and actual hatching of hayfield nests and (2) a 27-per-cent increase in the hatching of marsh nests between 1954 and 1955. The graph also shows that the hatching of hayfield nests lagged behind mowing at all dates for both 1954 and 1955, even though the 1955 season was earlier than the 1954 season.

The hatching of marsh nests preceded hayfield-nest hatching in June of 1954 and during most of the 1955 nesting season. This suggests that natural marsh vegetation may provide earlier nesting cover than the legume hayfields, or possibly that the hayfield nests, in part, may be renesting attempts by hens that had their earlier marshland nests destroyed.

Although few flushing bars were used, only five ducks were killed by mowing during 1954 and 1955. The reason for this low vulnerability to mowing is that dabbling

ducks generally rise swiftly and nearly vertically from the nest when flushed by the mowing machine, thus avoiding the cutting bar.

NEST PROTECTION

The nests that were protected in this study were located with a flushing rope. The flushing rope consisted of a double 50-foot length of three-eighths-inch hemp, with nine rock-filled cans suspended on 2-foot lengths of light chain uniformly spaced along the rope. The stretched flushing rope was dragged by two men through uncut hayfields, until each field was covered in a series of parallel strips. The dragging action of the rope on the vegetation, plus the noise produced by the rock-filled cans bouncing behind, flushed the hens. Hayfields were searched with the flushing rope one or two days prior to mowing; 243 acres of hayfields were searched in 1955.

In 179 acres of hay cruised after haying, it was found that only 39 of 68 mallard and blue-winged teal nests (57 per cent) had been located with the flushing rope prior to mowing. Bennett (1938), Earl (1950), and Sowls (1955) have experienced varying degrees of success in locating duck nests with flushing ropes similar in construction to the one used in this study.

During the 1955 nesting season, 33 blue-winged teal and 10 mallard nests were protected from haying. Thirty of these nests were left with unmowed islands of hay, nine were subjected to delayed cutting, and four nests were destroyed by mowing in spite of being carefully marked.

The nests to be protected by unmowed islands of hay were best marked by setting four stakes to form a square approximately 25 × 25 feet surrounding the nest. The islands were so staked that their sides formed 45° angles with the sides and ends of the fields. Staking of this type made mowing operations much easier, as the permittee had only to deviate 45° from his line of mowing, rather than an abrupt 90° had the island sides paralleled the field borders. Even this method did not solve the problem completely, as a few permittees mowed corners off the staked islands. The resulting nesting islands thus varied in size.

Of the 30 nests surrounded by various-sized islands of unmowed hay, 14 nests (47 per cent) hatched, 11 (37 per cent) were destroyed by mammalian predators or crows, and 5 (16 per cent) were abandoned. Variations in predator pressure between nesting areas may have influenced nest-island hatching success. Had all the nesting islands been 25 feet square or larger, the success figure might have been higher. This is supported by the fact that no nests hatched in islands that were 20 feet square or smaller (Fig. 2). Islands that were 25 feet square or larger

FIG. 2. Nesting islands smaller than 20 feet square were exceptionally vulnerable to predators. This island is approximately 10 × 20 feet in size.

had a 64 per cent hatching success. The increase in size between an island of hay 20 feet square and 25 feet square adds 255 square feet (56 per cent) to the over-all island area.

According to Bell (1954), seven duck nests were subjected to nesting-island management of this type on the state-controlled Horicon Marsh Wildlife Area in July of 1953. These nests were located at the time of mowing with the aid of a tractor-mounted Ohio-type flushing bar, operated under close supervision. Later checks showed that three of the nests were successful. Bell concluded that "a swath of 8 × 20 feet is the minimum size of uncut hay that should be left around the nest in order to provide sufficient protection from predators."

Although the sample sizes are small, the difference between my findings, which show that none of 14 nests surrounded by islands less than 20 feet square hatched, and Bell's hatching success of three out of seven nests can probably be explained by variation in predator pressure between the two areas.

Bennett (1938) suggested that islands of unmowed hay surrounding duck nests might attract "animals." Although one might expect unmowed islands of hay to offer special targets to mammalian predators, perhaps this is not the case. The discovery of an island of standing hay in a mowed field is probably the result of random wandering by the mammal. My data suggest that mammals more easily located nests in islands with an area of 20 feet square or smaller, than they did in islands with an area 25 feet square or larger—probably because the larger islands were less thoroughly searched. Since the hayfields were very dense and provided much overhead protection for the nests, crow predation was not serious unless the island was quite small in size.

Delayed cutting was employed only on 7.6 acres of hayfields during 1955, since the permittees did not readily accept the idea of leaving hay stand to insure the hatching of duck nests. Of the nine nests which were protected by delayed cutting, four hatched, three were destroyed by predators, and two were abandoned.

Combined data for the 43 duck nests protected from haying show that 18 (42 per cent) hatched, 14 (33 per cent) were destroyed by predators, 7 (16 per cent) were abandoned, and 4 were destroyed by mowing.

Disturbance by man and machine may have influenced the abandonment of nests, although most abandonment coincided with heavy, prolonged, cold rains in early June.

Mammalian predators — mainly skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), and opossum (*Didelphis marsupialis*)—caused 26 per cent of the nest mortality, while crows destroyed 7 per cent of the nests.

The 42-per-cent nest-hatching success for "managed" nests is within the range of nesting success found in other studies. Kalmbach (1939) found the average nest success, taken from the records of 22 field studies of waterfowl, to be 60 per cent. Bennett (1938) found the five-year average success for blue-winged teal nests in Iowa to be 59 per cent. On the same area, Glover (1956) found the nest success of bluewings to be 23 per cent in 1948 and 21 per cent in 1949. Earl (1950) found that the hatching success of mallards was 52 per cent in the Sacramento Valley, California.

A chi-square test showed the 25 per cent increase in nest success between 1954 and 1955 to be highly significant (Table 3). Seventeen per cent in this increase is the result of hayfield nest protection—particularly hayfield "islands," while the other 8 per cent in the increase can be credited to more nests hatching prior to haying in 1955.

TABLE 3. — COMPARISON OF 1954 AND 1955 MALLARD AND BLUE-WINGED TEAL HAYFIELD-NEST SUCCESS

Nests	1954		1955		1954-55	
	Number	Per Cent	Number	Per Cent	Number	Per Cent
Successful	14	14	41	39	55	27
Unsuccessful	85	86	65	61	150	73
Totals	99	100	106	100	205	100

DISCUSSION AND RECOMMENDATIONS

Since the Horicon National Wildlife Refuge is managed primarily for Canada geese, major emphasis has been placed on the farm program in order to produce waterfowl food in the form of agricultural crops. This means that crop production has received priority over nesting when hayfields are considered, since hay enters into the crop-rotation plan.

Certain management proposals appear to have some potential for reducing the destruction of waterfowl nests by haying operations. Hayfield-island protection for duck nests is not feasible on a large scale, because it is difficult to locate the nests in hayfields prior to mowing.

An alternative method for protecting nests is delayed cutting. Delayed cutting, however, opposes proper legume-haying techniques. Cutting at the early bloom stages produces an excellent quality hay, with a high protein and ash content and a low fiber content (Smith, 1956). If the first cutting in this region should be delayed until after July 15, when the majority of hayfield nests should be terminated (Fig. 1), the resulting hay would be of far less value as livestock feed due to the loss of nutrients and the increased fiber content. The hay crop would then have to be cut and removed from the field so that a second crop could be harvested. Since it has been the practice of the permittee to take all of the hay as a part of his crop-division share, he would have to be compensated for the total or partial loss of the first hay crop. Refuge budgeting does not permit monetary allowances for such losses. The compensation to the permittee would be in the form of a larger share of either corn or grain produced on the refuge farm units. This would result in a smaller amount of corn that could be left on the refuge farm units as feed for migrating ducks and geese. On a corn-exchange basis, the refuge would be required to give the permittee 20 to 25 bushels of corn, at current prices, for each acre of legume hay on which cutting was delayed. Thus a plan restricting the first hay cutting on all refuge farm units, until the majority of the hayfield nests had hatched, certainly would not be a feasible practice under present conditions.

A proposal restricting hay cutting within 30 yards of the field edge, until after the hatching peak, would also reduce nest mortality. This plan is based on the fact that 76 per cent of the nests found in this study were located within 30 yards of the field edge. However, because much of the refuge farm land is managed on 30-yard cropping strips alternated with 10-foot grass buffer strips, this plan would practically eliminate the first hay cutting on many farm units.

The 1954-55 data show that duck-nest densities were highest in hayfields nearest the marsh; this resulted from the lack of wild nesting habitat between the cropland and the marsh edge. Approximately 90 per cent of the duck nesting on the refuge hayfields during 1954 and 1955 occurred along three miles of farm units located immediately adjacent to the marsh. These are the farm units that should receive the most intensive management. It seems most feasible to manage the hayfields possessing high duck-nest densities specifically for nesting.

A delayed-cutting program applied to hayfields with high nest densities would not complicate the management of the entire farm-unit system. The land-use permits should be amended to include a provision allowing the permittees to be compensated by a larger share of either grain or corn *if* the first cutting of hay should be delayed.

It might be possible to eliminate the compensation principle entirely if the permittees could be encouraged to grow the first legume-hay crop for seed. Several very successful alfalfa and red clover seed crops were produced in the Horicon area during 1954 and 1955. The seed crop would take the place of the first hay cutting thus requiring no modification of the share-cropping system. The seed harvest would occur well past the hayfield-duck hatching period, and thus reduce nest destruction to a minimum.

The remaining alternative for reducing hayfield nest losses would involve a change in refuge policy, whereby all farming would be carried on by the refuge staff.

ACKNOWLEDGMENTS

The financial assistance for this study was provided by the U.S. Fish and Wildlife Service and the Wisconsin Alumni Research Foundation.

I would like to express my thanks to the following personnel at the Horicon National Wildlife Refuge: Lloyd F. Gunther, manager, for constructive criticism and encouragement of the project; C. A. Hughlett, assistant manager, for keen interest and assistance in the field; and Harold Bushweiler, clerk, for clerical help.

Many farm-unit permittees—particularly Clarence Sterr—gave much-appreciated assistance in practices directed toward reducing hayfield-nest mortality. R. A. McCabe and J. J. Hickey contributed advice throughout the study. Frederick Greeley gave many helpful suggestions during the writing of the paper.

SUMMARY

At the Horicon National Wildlife Refuge in Wisconsin, farm units have been managed on a share-cropping basis with farmer permittees; all of the legume hay goes to the permittees so that the refuge can retain as much corn as possible to feed migratory ducks and geese.

In 1954-55, the duck-nesting density was approximately one nest per three acres of legume hay. Mowing of the first legume-hay crops preceded the major period of hayfield-duck hatching for both years, causing 100 per cent destruction of all hayfield nests active at that time.

Islands of uncut hay—25 feet square or larger—surrounding duck nests allowed a hatching success of 64 per cent, but duck nests were difficult to find and a flushing rope was only 57 per cent efficient.

Ninety per cent of the hayfield-duck nests were concentrated along three miles of farm units located immediately adjacent to the marsh. Under existing management policies for this refuge, the soundest recommendation to reduce hayfield-nest mortality is to manage the farm units with high nesting densities specifically for nesting ducks. This would involve delaying the first hay cutting until the majority of the nests had hatched. The permittees of these particular farm units would have to be compensated for the total or partial loss of the first legume-hay crop by a larger share of refuge-grown corn or grain. Growing the first legume-hay crop for seed may provide the solution to reducing hayfield-nest mortality under the farmer-permittee system.

LITERATURE CITED

BELL, J. 1954. Hay or game . . . or both? Wis. Cons. Bull., 19(6):22-23.

BENNETT, L. J. 1938. The blue-winged teal: its ecology and management. Collegiate Press, Ames, 144pp.

EARL, J. P. 1950. Production of mallards on irrigated land in the Sacramento Valley, California. J. Wildl. Mgmt., 14(3):332-342.

ENGLISH, P. F. 1934. Game bird flushing apparatus. Mich. Dept. Cons., Game Bull. No. 2, 8pp.

GIRARD, G. L. 1941. The mallard: its management in western Montana. J. Wildl. Mgmt., 5(3): 233-259.

GLOVER, F. A. 1956. Nesting and production of the blue-winged teal (*Anas discors* Linnaeus) in northeast Iowa. J. Wildl. Mgmt., 20(1):28-46.

GOLLOP, J. B. AND W. H. MARSHALL. 1954. A guide for aging duck broods in the field. Report for Mississippi Flyway Technical Section, 14pp., mimeo.

GUNTHER, L. F. 1954. Horicon National Wildlife Refuge narrative report. September-December. (Unpublished quarterly report, U.S. Fish and Wildl. Serv.) 39pp.

KALMBACH, E. R. 1939. Nesting success: its significance in waterfowl reproduction. Trans. N. Amer. Wildl. Conf., 4:591-604.

SMITH, D. 1956. Cutting alfalfa early for better quality hay and silage. Agric. Exp. Sta., U. Wis., Madison, Bull. 521, 4pp.

SOWLS, L. K. 1955. Prairie ducks. Stackpole Co., Harrisburg, 193pp.

Received for publication June 12, 1956.

GALVANOTAXIC RESPONSE OF FISH TO PULSATING DIRECT CURRENT[1]

Glenn N. Taylor,[2] Larry S. Cole,[3] and William F. Sigler[4]

Utah State Agricultural College, Logan, Utah

Introduction

Purpose of the Problem

Electrical shocking of fish has considerable practical application in stream survey work for its ease of capturing a majority of fish in a section of stream. The shocker uses either alternating or direct current. The latter is applied as a continuous-power flow or in pulses of varying-voltage shapes and durations. This paper summarizes an investigation of the advantages and disadvantages of some power forms, especially that of pulsed direct current, in capturing live fish. Such information may aid in developing a more efficient fish-collecting device.

Review of the Literature

The first practical application of electricity in fisheries work was probably the electric fish stop. As early as 1917, H. T. Burkey applied for a patent on an electric fish screen, and in 1928 he proposed the use of voltage impulses in directing the movement of fish. A comprehensive study on the development of the electrical fish screen was presented by Holmes (1948).

Electrical fishing necessarily includes numerous scientific fields. A bibliography published by the Fish and Wildlife Service (Applegate, *et al.*, 1954) is of great help in locating some of the widely dispersed material. However, in spite of numerous data relative to the various phases of electrical fishing, the amount of material evaluating the use of pulsed direct current at various pulse rates, duty cycles[5] and wave shapes is limited. A study by McLain and Nielsen (1953) dealing with pulsed direct current employed a square wave and three different duty cycles. Their publications presented the results of only low-pulse frequencies with the other conditions constant, and they did not vary the pulse frequency such that the effect of various pulse rates could be determined. No studies were found relative to a triangular voltage pulse used with a variable duty cycle and pulse rate.

Materials and Methods

Nature of the Problem

This study is primarily an evaluation of the galvanotaxic properties of direct current pulsed in triangular voltage waves. However, enough tests using continuous direct current and alternating current were conducted under identical conditions so that a comparison can be made. The data presented deal principally with voltage gradient, duty cycle, and frequency of pulse required to produce a given response. Records were also kept of fish injury and mortality as they were observed during the experiments. Also, intentional attempts were made to produce injury by electrical shock to the fish; this experiment was followed by X-ray studies and gross and histological examinations of tissue specimens.

Description of the Equipment

The controlled-shocking experiments were conducted in a ¾-inch marine-plywood tank 2 feet deep, 5 feet wide and 12 feet long (Figs. 1 and 2). The tank was reinforced with steel angles and the interior painted white with a nonconductor water-repellent paint. Two large metal trays, one at each end, served as the electrodes. A plastic screen at each end of the tank prevented

---

[1]Joint contribution from the Department of Wildlife Management, Utah Cooperative Wildlife Research Unit, Engineering Experiment Station. Abstract from thesis for M.S. degree in Wildlife Management, Utah State Agricultural College, 1955.

[2]Former graduate student, Wildlife Management Department; present address: University of Utah School of Medicine, Salt Lake City, Utah.

[3]Professor and Head, Department of Electrical Engineering.

[4]Professor and Head, Department of Wildlife Management.

[5]Duty cycle is the ratio of the length of time the circuit is closed to the total length of the cycle.

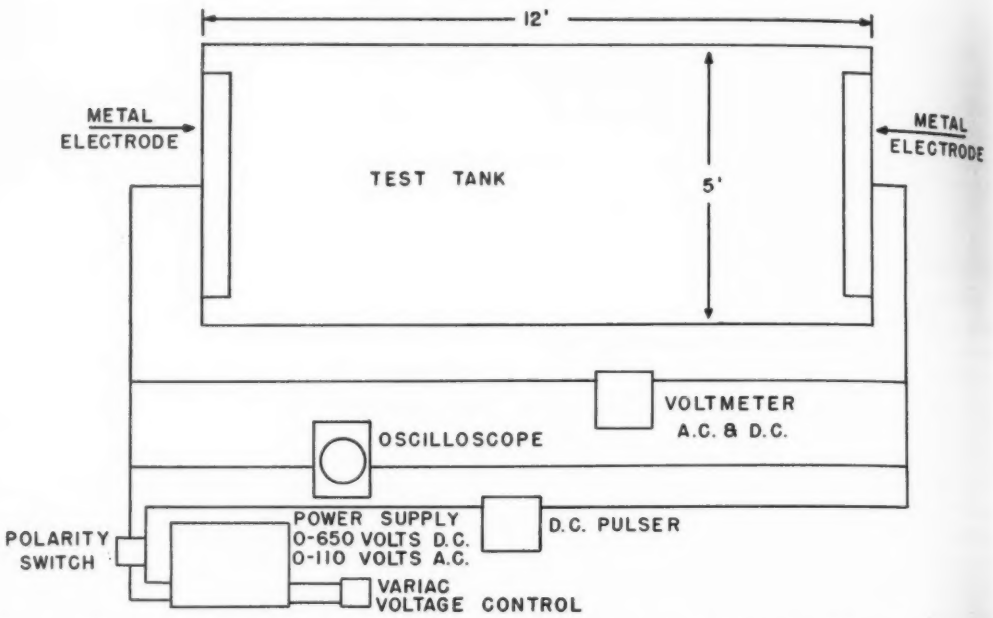


FIG. 1. Diagram of test tank and electrical equipment used in the AC, steady DC, and pulsed DC shocking experiments.

fish from coming in direct contact with the electrodes.

The electrical power supply was from the city line (110 volts, 60-cycle, alternating current). A variac, transformer, and rectifier made it possible to obtain direct-current peak voltages from 0 to 650 volts (Fig. 3). The same equipment was used for the continuous direct-current tests as for the pulsating-current tests except that the motor-driven breaker points remained closed with continuous current (Fig. 3). During experiments with alternating current a line from the city power supply, controlled by a variac, was wired directly to the tank. Voltage measurements for alternating and continuous direct current were made with a high-resistance AC and/or DC volt meter, and voltages during pulsed direct-current experiments were read on the calibrated screen of an oscilloscope. The oscilloscope also was used to determine the voltage wave shape.

Techniques and Methods Employed

Most of the electrical-shocking experiments were conducted at the Utah Department of Fish and Game hatchery located near Logan, Utah. All fish used, except where specifically designated otherwise, were rainbow trout (*Salmo gairdneri*).

The water used in these experiments was from an artesian well that had a temperature of 57° F. and a resistance of 1,700 ohms per cubic inch. The water depth in the tank was maintained at one foot during all tests. Since the flow of water through the tank was not continuous, aeration and temperature were controlled by periodic changings. Water temperature during the tests was allowed to vary between 60° and 64° F. However, this variation in temperature, and even greater differences in temperature, should not have influenced the response of the fish, according to the work of McLain and Nielsen (1953).

Preliminary tests using a volt meter attached to two small electrodes spaced one foot apart indicated that the electrical field within the tank was uniform. This condition made it possible to compute the voltage per inch that would apply to any area in the tank by dividing the distance in inches separating the electrodes at each end into the potential difference across the tank during the various tests. This was the procedure used in determining the voltage gradient as given in this paper.

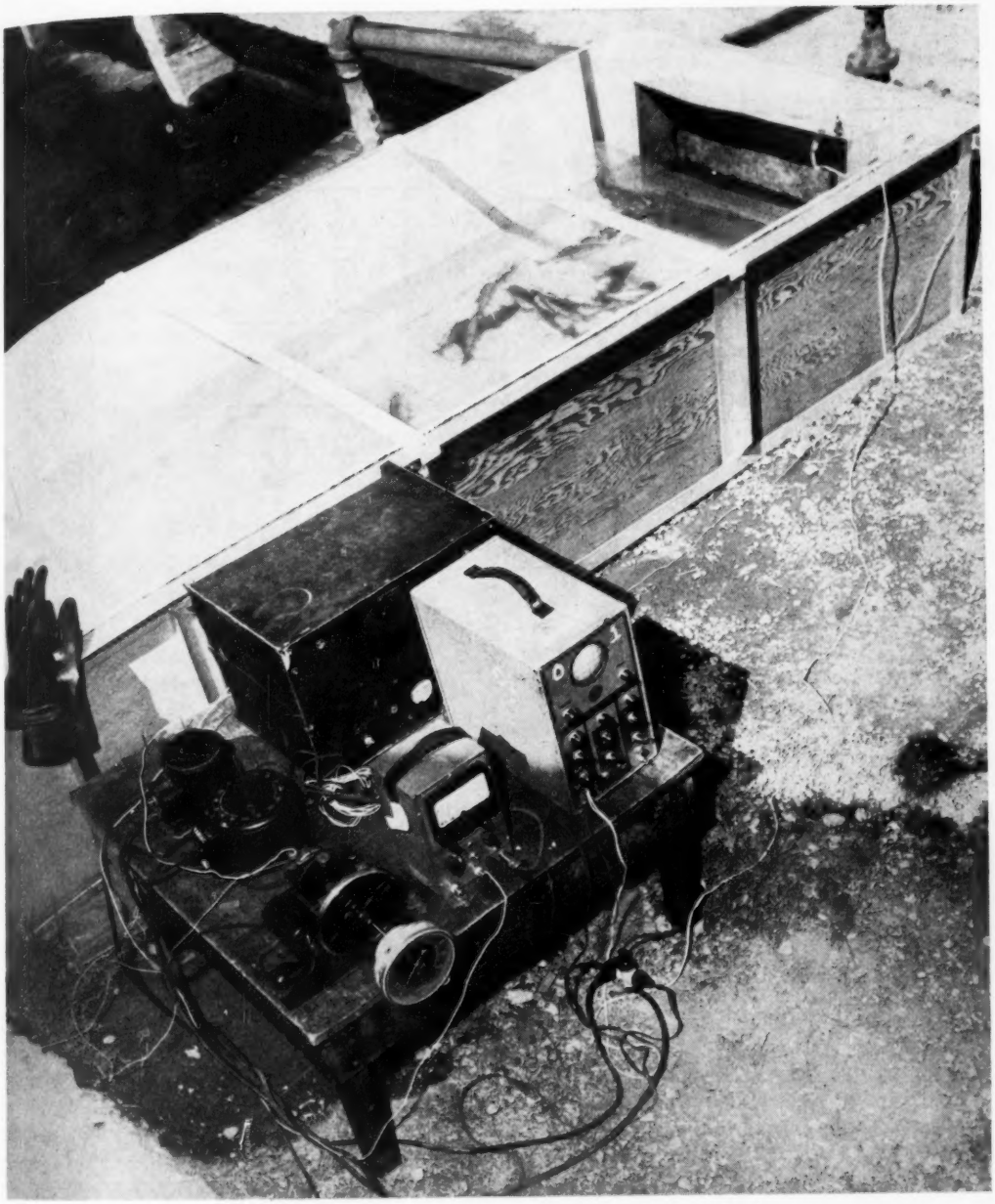


FIG. 2. Electrical equipment and the tank used in the controlled shocking experiments.

The shape of the voltage wave was determined in all tests with an oscilloscope, wired to the electrodes at each end of the tank. For the 60-cycle alternating current the form was a typical sine wave; for the pulsed direct current the form was triangular, varying in shape with the frequency—tending to be less acute at lower frequencies; and for continuous direct current the wave had a slight undulation but for all practical purposes was a straight line.

It would have been desirable, from the standpoint of eliminating a variable, not to shock the same fish more than once, but

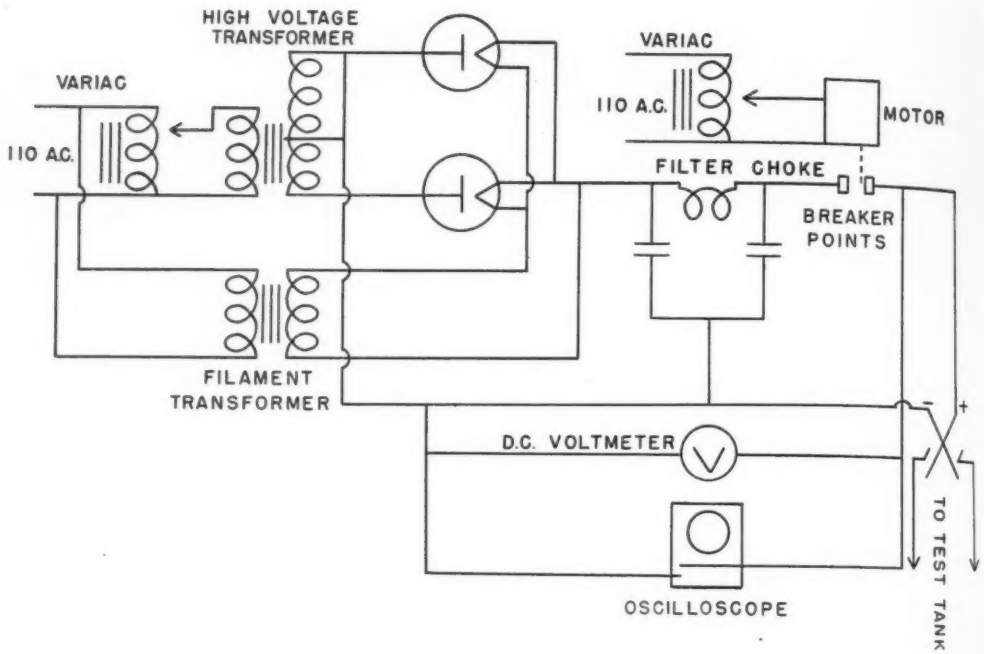


FIG. 3. Diagram of electrical equipment used in the continuous DC and pulsed DC tests.

difficulties involved in such a segregation made this impractical. However, prior to the shocking experiments of any one day, sufficient fish within the given length class were captured and placed within a live box adjacent to the tank. This segregation prevented the same fish from being shocked twice during a given day. Also, since a relatively small number of fish were selected from and returned to a school containing approximately 10,000 fish the odds are slight that the same fish was used more than once.

Prior to placing the fish in the tank, the voltage, frequency, and duty cycle were set so that the response observed was the result of only one set of conditions. In all instances, except where mentioned, at least five fish of approximately the same length were used in each test. These were placed in the tank and given sufficient time to adjust to the new environment. Then a switch was closed subjecting them to the previously arranged stimulus, and the reaction to the electrical field was determined. To facilitate removal of the fish from the tank, the voltage was raised to the electronarcotic level, and the fish were removed with an insulated dip net. This procedure not only facilitated removal of all specimens from the tank, but also it gave us a considerable number of fish subjected to relatively high voltages from which injury data could be noted.

A further test to determine some of the physical injuries that might be received by fish exposed to relatively high voltages was conducted by killing an 8-inch fish with alternating current and then immediately preparing the organs of the fish for histological study. The same tissues and organs were taken from a normal 8-inch fish and prepared in a similar manner. This duplication was necessary since we were unable to find any sufficiently detailed studies that dealt with the microanatomy of a normal rainbow trout.

In addition to the tissue-section examination, three fish (12 inches, 14 inches, 14 inches) were killed with an alternating current, after which X-rays were taken to determine any changes of the bone structure.

Because of small losses resulting from continuous direct current and from pulsed direct current, only the injurious effects of alternating current were examined in detail.

TABLE 1. — GALVANOTAXIC RESPONSE OF SIX LENGTH CLASSES OF RAINBOW TROUT TO STEADY DIRECT CURRENT AT A WATER TEMPERATURE OF 65° F.; MEASURED IN FIVE CLASSES OF RESPONSE FROM 0, REPRESENTING NO RESPONSE, TO 5 FOR COMPLETE PARALYSIS[1]

Length-class Size (inches)	2-3	4-5	6-7	8-9	10-11	12-13
No. of Fish Shocked	51	130	23	85	6	4
Voltage Gradient (volts per inch)	Coded Response					
0.26	0	0	0	0	1	–
0.31	0	0	0	1	1	2
0.37	0	0	1	2	2	2
0.42	0	0	0	2	3	2
0.47	1	2	1	3	3	2
0.52	1	2	2	3	3	3
0.57	0	2	2	3	4	3
0.62	0	2	2	3	3	–
0.67	0	2	3	3	3	–
0.72	0	3	3	3	3	–
0.77	0	3	3	3	3	–
0.82	1	3	3	3	3	–
0.87	1	3	3	3	4	4
0.92	2	3	3	3	4	4
0.97	2	3	3	3	4	4
1.02	3	3	3	3	4	4
1.07	3	3	3	4	–	–
1.12	3	3	4	–	–	–
1.17	3	3	–	–	–	–
1.22	3	4	–	–	–	–
1.27	3	4	–	–	–	–
1.32	4	–	–	–	–	–
1.37	4	–	–	–	–	–

[1]Code:
0 = no polarity or distress
1 = slight galvanotaxis and alignment along equipotential planes, shivering and signs of minor distress
2 = fair galvanotaxis; immediate movement to pole at the initial shock but usually escapes
3 = strong determined movement to pole; no paralysis in less than 7 seconds
4 = complete paralysis in 6 seconds or less, and usually it did not reach the positive pole

RESULTS

Experiments with Rainbow Trout

The following data include tests with 60-cycle alternating current, uninterrupted direct current, and pulsed direct current. Pulses of 0.33, 0.47, and 0.88 duty cycle were used at frequencies from 2 per second to 120 per second. A total of 1,812 fish was used in the experiments with an average of 5 tested at each voltage, duty cycle, and pulse frequency combination. Responses were arbitrarily divided into five different groupings that are defined in the tables under the designation "code." The same code was used for all of the tests with direct current, but not for those in which alternating current was employed. Here it was necessary to use different designations since there is no galvanotaxic response with this form of power. From the standpoint of a collecting device, the number-three response represents the primary criterion for judging efficiency of the shocking operation.

Relationship of body length and response. The data given in Table 1 and Fig. 4 were determined for the purpose of evaluating the relationship between the degree of response of a fish exposed to a continuous direct-current electrical stimulus and its body length. The voltage gradient was mea-

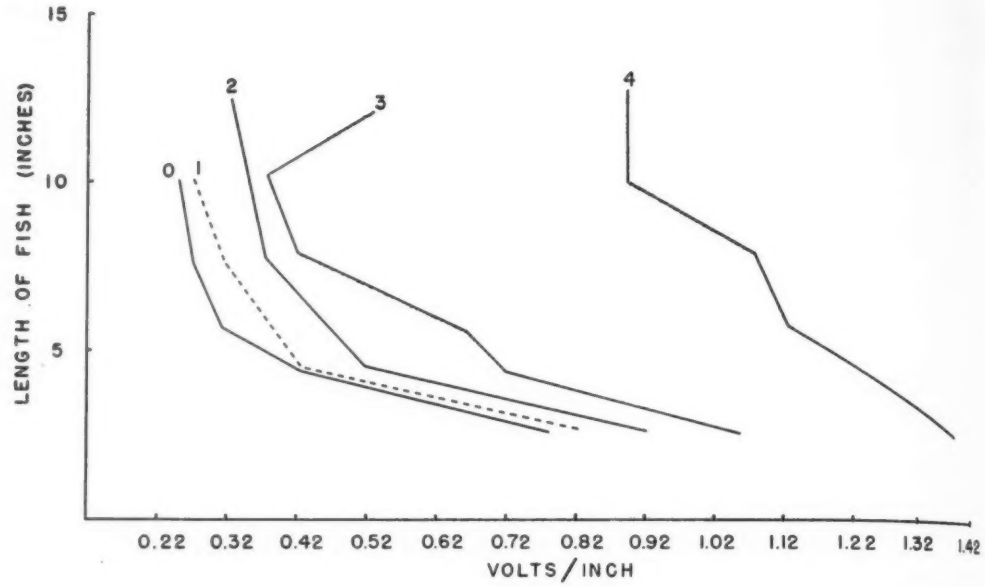


FIG. 4. Responses obtained in a given length class of rainbow trout at various voltages when using continuous direct current (see Table 1 for code and numerical values).

sured as the potential difference between two points (one inch in this instance) on a line drawn perpendicular to and joining the electrodes at each end of the tank. The following significant observations were noted:

1. The voltage range through which a good galvanotaxic response was obtained (the voltage difference between the number-two and number-four response) tended to increase as the length of the fish increased, with one exception—the 12-inch fish that caused the number-three curve shown in Fig. 4 to veer back to the right. However, this was very likely an individual variation since it is the only example that did not follow the general pattern, and also since it is at variance with the curve representing the number-two response, as shown in the same figure.

2. The severity of any voltage gradient increased with the length of the fish.

3. It has been observed in our stream-survey work that a variable percentage of the fish are not captured since they are frightened away by coming in contact with the "fringe area," which is the part of the electrical field that is too weak to cause galvanotaxis, but strong enough to stimulate the fish—usually away from the areas of the field that are more intensely charged. This study indicates that the voltage gradient of the "fringe area" probably lies somewhere between or includes the voltages necessary to cause the number-one and the number-two responses (Table 1).

4. A high degree of selectivity was possible when sampling mixed-length classes of fish (Fig. 4). A voltage sufficient to cause galvanotaxis in one length class might merely constitute a fringe gradient for a smaller fish.

Direct current tests using 0.33 duty cycle. Table 2 and Fig. 5 contain the results of the experiments employing pulsed direct current, an 0.33 duty cycle, and a triangular-wave shape. The length of the pulses varied from approximately 28 milliseconds at 12 pulses per second through 3 milliseconds at 120 pulses per second. The duration of the interval between pulses varied from 55 milliseconds at 12 pulses per second through 6 milliseconds at 120 pulses per second. The following significant observations were noted:

1. The voltage gradient required to cause a good leading response diminished as the pulse frequency was increased from 12

TABLE 2.— GALVANOTAXIC RESPONSE OF 8- TO 9-INCH RAINBOW TROUT TO PULSATED DIRECT CURRENT, USING AN 0.33 DUTY CYCLE. THE RESPONSE IS REPRESENTED BY THE CODE NUMBER GIVEN IMMEDIATELY BELOW THE RESPECTIVE VOLTAGE GRADIENT. (SEE TABLE 1 FOR CODE.)

Pulses/ Second	12	24	36	48	60	72	84	96	120
Voltage Gradient in Volts per Inch									
	0.15	0.30	0.21	0.20	0.19	0.17	0.16	0.15	0.15
	0	0	0	1	0	0	0	1	0
	0.45	0.49	0.45	0.38	0.38	0.42	0.26	0.30	0.30
	1	0	1	1	2	1	1	2	2
	0.76	0.53	0.49	0.49	0.42	0.64	0.45	0.45	0.45
	1	0	1	1	2	2	2	1	1
	0.98	0.68	0.61	0.57	0.61	0.83	0.53	0.57	0.57
	1	0	1	2	2	3	2	2	1
	1.29	0.83	0.76	0.76	0.68	1.02	0.61	0.64	0.64
	2	1	1	2	2	4	2	3	2
	1.52	0.98	0.91	0.83	0.83	1.25	0.68	0.68	0.68
	2	1	2	3	3	3	3	3	3
	1.82	1.14	1.06	0.98	0.91	1.44	0.76	0.75	0.75
	2	2	2	3	3	4	3	3	3
	2.20	1.29	1.14	1.06	0.98		0.91	0.83	0.83
	3	1	2	3	3		3	3	4
	2.58	1.36	1.21	1.14	1.10		0.98	0.91	0.91
	3	2	3	3	3		3	3	3
	2.61	1.44	1.36	1.33	1.21		1.06	0.98	0.98
	3	2	3	3	3		4	3	4
	2.73	1.59	1.52	1.52	1.36		1.15	1.06	1.21
	3	1	3	3	4		4	4	4
	2.88	1.74	1.67	1.59	1.40		1.29	1.21	1.36
	3	2	3	3	4		3	3	4
	3.65	1.97	1.82	1.67	1.52		1.36	1.36	1.48
	3	3	3	4	4		4	4	4
	3.79	2.12	1.97	1.74					
	3	3	3	4					
	3.90	2.35	2.12	1.89					
	4	3	4	4					
		2.50	2.27	2.05					
		2	4	4					
		2.58	2.35						
		3	4						
		2.65							
		3							
		2.84							
		4							
		2.99							
		3							
		3.33							
		4							
		3.41							
		4							

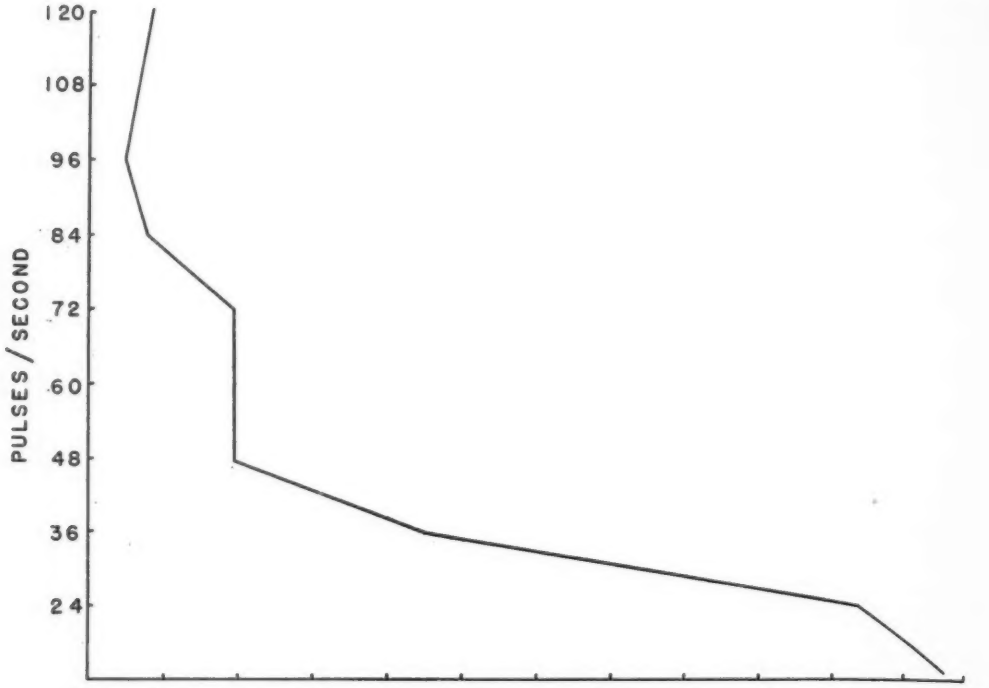


FIG. 5. Voltage gradient and pulse frequency required to produce a good (code number three) galvanotaxic response with 0.33 duty cycle, using 8- to 9-inch fish.

pulses per second to 96 pulses per second. Between 96 pulses per second and 120 pulses per second a slight increase in gradient was necessary to cause a good galvanotaxic response.

2. The most efficient leading response occurred at a frequency of 96 pulses per second. At this rate the voltage necessary to cause a good galvanotaxic reaction was reduced to 45 per cent of that needed to cause a similar response when using continuous direct current with the same length class of fish. The pulse duration and the interval between pulses was approximately 4 milliseconds and 8 milliseconds, respectively, at this optimum frequency.

3. The most pronounced effect relative to voltage gradient necessary to cause galvanotaxis occurred between the pulse rates of 12 and 48 per second.

4. Pulse frequencies between 48 per second and 72 per second were similar in effect.

5. The voltage range through which fish showed a good galvanotaxic response diminished as the frequency increased. This tended to reduce the voltage interval between the number-two and the number-four responses.

Direct current tests using 0.47 and 0.88 duty cycles. Tests using 0.47 and 0.88 duty cycles at various frequencies were conducted only to the extent that it was determined that such duty cycles tended to be less efficient than the 0.33. The data from these tests are not included in this paper.

Comparison of pulsed and steady direct current. This study involves the relationship of steady direct current to pulsed direct current as a means of collecting fish. This comparison was possible since the same code numbers and techniques were used in designating the various responses observed in the experiments utilizing both forms of

TABLE 3. — THE RELATIONSHIP BETWEEN THE MINIMUM STEADY DIRECT CURRENT VOLTAGE AND THE MINIMUM PULSATED DIRECT CURRENT VOLTAGE REQUIRED TO STIMULATE 8-IN. FISHES TO ELICIT A GOOD (CODE NUMBER THREE) RESPONSE[1]

Duty Cycle	Pulses/Second	Minimum Voltage Causing a Good (Code No. 3) Response: (V peak) peak DC volts/inch	Minimum Voltage Causing a Good (Code No. 3) Response: (V eff) effective steady DC volts/inch	Watts
Steady DC	—	0.47	0.47	9.9
0.33	12	2.20	0.73	23.6
	24	1.97	0.66	19.5
	36	1.21	0.40	7.2
	48	0.83	0.24	2.7
	60	0.83	0.24	2.7
	72	0.83	0.24	2.7
	84	0.68	0.22	2.2
	96	0.64	0.21	2.0
	120	0.68	0.22	2.2

[1]This table also gives a comparison of the minimum power required to cause a good (code number three) response.

current. To make such a comparison possible, the voltages shown in the tables relative to pulsating current, which are the peak voltages as observed on an oscilloscope screen, were converted to the equivalent value in terms of steady direct current by means of the following relationship (for a triangular-voltage pulse):

$$V_{eff} = V_{peak}\left[\frac{t_o}{3T}\right]\frac{1}{2}$$

V_{eff} = continuous direct current equivalent voltage
V_{peak} = peak voltage of pulse
T = period of cycle
t_o = duration of pulse

The equivalent voltages as determined by the above formula, the voltages for steady direct current, and the power values, all of which represent minimum values necessary to cause a good galvanotaxic (code number three) response are summarized in Table 3. An analysis of these data indicates that the efficiency of a continuous direct-current shocking machine may be increased through the use of relatively rapid pulses, an 0.33 duty cycle, and a triangular-voltage pulse. Also, power, expressed as watts, decreases with an increase of frequency of pulses per second. The power was computed for the entire tank having a water depth of one foot and water resistance of 1,700 ohms per cubic inch.

Alternating current tests. Alternating current was used on 8- to 9-inch fish in such a way that the voltage required to capture fish with alternating current could be compared with the voltage causing galvanotaxis of the same size fish by using continuous direct current, and pulsed direct current (Table 4).

For comparative purposes, the alternating-current voltage, 0.57 volts rms per inch, shown above the number-four code response

TABLE 4. — THE RESPONSE OF 8- TO 9-INCH RAINBOW TROUT TO 60-CYCLE ALTERNATING CURRENT IN WATER 60° TO 63° F.

Voltage Gradient (rms volts per inch)	Coded Response[1]
0.26	1
0.31	2
0.37	2
0.42	2
0.47	3
0.52	3
0.57	4
0.62	5
0.67	5

[1]Code:
1 = no response
2 = irritation and alignment on equal potential planes
3 = slight paralysis
4 = paralysis in 7 or more seconds
5 = paralysis in 6 seconds or less

in the following chart, is used since it is probably the minimum voltage, as indicated by this study, that will capture fish of the given-length class. The above figure, 0.57 volts rms per inch, should be reduced slightly when comparing it with the data in Table 3, since the equivalent voltage in terms of direct current will be slightly lower. Comparison with Table 3 indicates that in terms of the voltage per inch required, the continuous direct current and the pulsed direct current, with the exception of the 0.88 duty cycle, are more efficient than the alternating current. Also, in a comparison of the voltage required for a paralytic response, the direct current pulsed at high frequencies was still more efficient than the alternating current.

Experiments with Species Other than Rainbow Trout

Preliminary tests using continuous DC and pulsating DC were conducted to determine the galvanotaxic response of carp (*Cyprinus carpio*), channel catfish (*Ictalurus punctatus*), Rocky Mountain whitefish (*Coregonus williamsoni*), and the Utah sucker (*Catostomus ardens*). With the exception of the Utah sucker, at least a fair leading response was observed in all of the above species. These tests were too brief to compare the duty cycle, pulse frequency and voltage necessary to cause a similar response in rainbow trout.

EFFECTS OF ELECTRICAL SHOCK ON FISH

Mortality Rate

The voltage was increased, following the respective tests, to exceed the electronarcotic level to facilitate removal of fish from the test tank. This procedure necessarily exposed the fish to relatively high voltages—higher than they would usually receive in routine stream-survey work. The resulting mortality figures (Table 5) suggest that alternating current causes a higher mortality than direct current (pulsed or steady). This same trend has been observed by the writers when collecting fish with electricity under natural stream conditions.

Tissue Alterations

One 9-inch trout was intentionally killed in the test tank with 60-cycle alternating current by gradually increasing the voltage

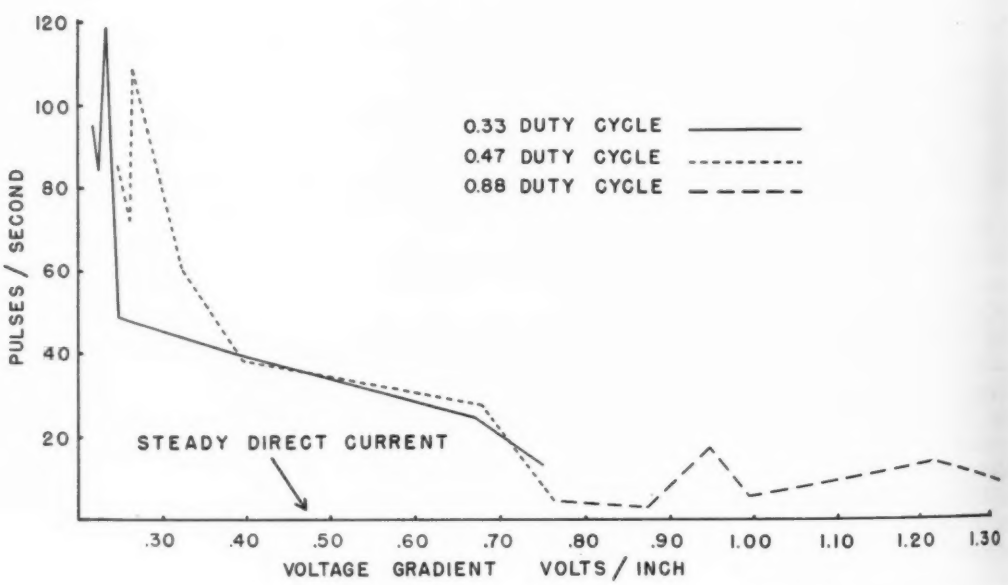


FIG. 6. A comparison of steady direct current, and pulsed direct current of 0.33 duty cycle. The curve for 0.33 duty cycle and the point indicated for steady direct current show the voltage-frequency combination necessary to cause a good galvanotaxic response.

TABLE 5. — FISH MORTALITY RATES

Form of Power	Number of Fish Shocked	Number of Fish Killed	Per Cent Mortality
Uninterrupted DC	91	0	0
Pulsed DC	1,641	5	0.3
60-cycle AC	46	2	4.2

to 1 volt per inch over a period of 3 seconds and leaving the fish thus exposed for another 6 seconds. Following electrocution, the fish was left for 10 minutes in a holding box to be sure it was dead, after which post-mortem observations were made. No sign of injury could be grossly detected.

Immediately after the post-mortem the following organs and tissues were fixed in 10 per cent Formalin and later sectioned, mounted on slides, and stained with hematoxylin and eosin:

eye
liver
gill
heart
ovary
spleen
pharynx
intestine (4 inches from pylorus)
duodenal process
brain
bulbus arteriosus
skeletal muscle (immediately posterior to pectoral fin)
skeletal muscle (lateral line between pelvic and dorsal fin)
stomach
skin (dorsal aspect of head)
lateral line nerve
lower intestine (¾-inch from cloaca)
spinal cord (ventral to adipose fin).

Also, the same organs and tissues were taken from a normal fish and prepared in a similar manner.

A total of 797 H & E sections, about equally divided between the control fish and the electrocuted fish, were made and examined microscopically. No abnormality in any of the above tissues was found.

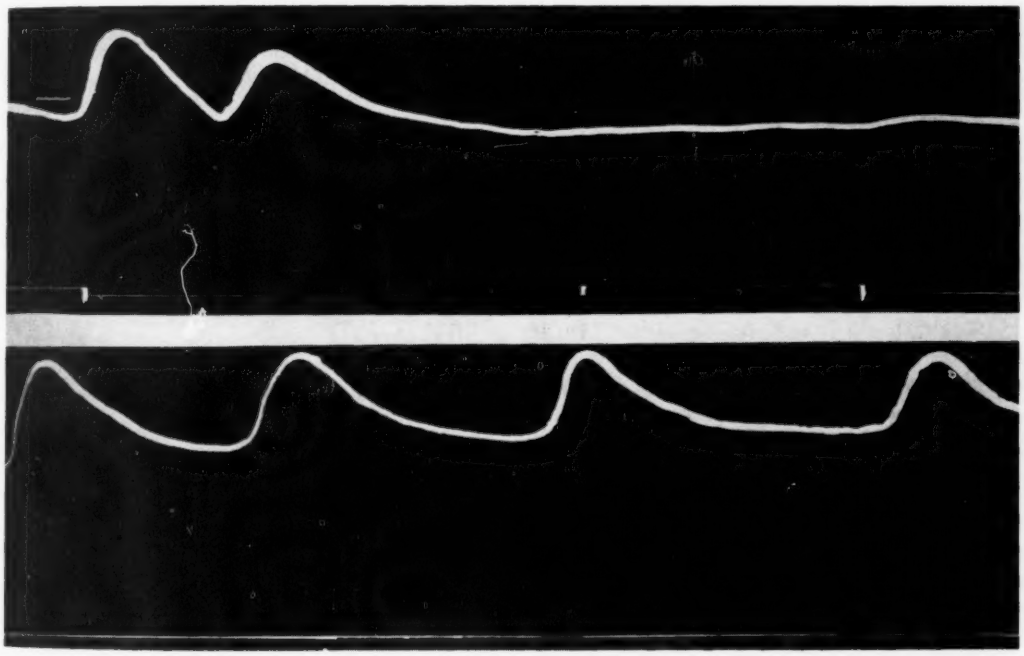


FIG. 7. Kymogram showing the heart action of a 9-inch rainbow trout during direct stimulation with a tetanizing current. The base line indicates when the circuit is closed or open, being in the low position when closed. The lower tracing is a continuation of the upper tracing and the circuit is closed.

Damage to Bone Structure as Determined by X-ray

Three fish (12-inch, 14-inch, and 14-inch) were killed with alternating current in the test tank. A fourth fish, 10 inches long, to be used as a control, was suffocated. These specimens were then X-rayed.

Of the three electrocuted fish, only the largest showed injury. One vertebra had a compression fracture and the next posterior vertebra showed a fracture and injury to the dorsal spinous process. Also, the spinal column was luxated at an intervertebral disc. Soft-tissue damage was also evident in the area immediately ventral to the damaged vertebra, as a result of 6 ribs being torn free from their vertebral attachments. Considerable extravasated blood was present in the intercostal tissue in the region of the disarticulated ribs. A subcutaneous hematoma was evident on the side about an inch ventral to the dorsal fin and could be seen grossly before dissection. All of the above observations were further substantiated by post-mortem dissection.

This study, with the exception of the 14-inch fish, did not disclose the high percentage of physical distortions resulting from electrical shock as observed by other investigators. In most instances death appeared to be due, in part, to respiratory paralysis. That the heart is probably not severely affected can be seen in the following kymogram (Fig. 7) in which the heart action is recorded during stimulation with a tetanizing current. The heart missed several beats but soon resumed a regular pace even while being stimulated. Death resulting from electric shock is in most instances probably the result of physiological factors and not ruptured blood vessels, damage to bones, or other trauma. This is seen in instances in which fish are occasionally killed with continuous direct current which does not cause the severe spasms and tetany that are seen when one is using alternating current and pulsed direct current.

As a result of this study, it appears to the writers that in fish less than 12 inches long the primary cause or causes of death resulting from electrical shock are physiological and only occasionally due to injuries that can be observed grossly or microscopically.

SUMMARY

The galvanotaxic response of fish to continuous direct current and pulsating direct current, using 0.33, 0.47, and 0.88 duty cycles with a triangular voltage wave shape was investigated. The reaction to alternating current was also studied.

Employing pulsed direct current, the most efficient leading response occurred when using an 0.33 duty cycle, pulsed at 96 times per second. With this type of current the voltage necessary to cause a good galvanotaxic response was reduced to 45 per cent of that necessary to cause a similar response when using continuous direct current, and the power was reduced to 20 per cent of that necessary to cause a similar response with continuous direct current.

Tests using 0.47 and 0.88 duty cycle indicated that these tended to be less efficient than the 0.33 duty cycle.

Observations concerning the harmful effects to the fish resulting from the electrical shocks indicated that losses when using steady direct current or pulsed direct current are insignificant. It was also noted that direct current (steady or pulsed) is safer than alternating current. No losses occurred in shocking 91 fish with continuous direct current; 0.3 per cent mortality occurred in shocking 1,641 fish with pulsed direct current; and 4.2 per cent mortality occurred in shocking 46 fish with alternating current. The cause of death in most instances appeared to be from factors that could not be observed either grossly or microscopically.

In conclusion, this study indicates that the efficiency of a direct-current machine can be increased through the use of triangular-shaped voltage pulses, 0.33 duty cycle, and a relatively fast pulse rate.

LITERATURE CITED

APPLEGATE, VERNON C., PAUL T. MACY, AND VIRGIL E. HARRIS. 1954. Selected bibliography on the applications of electricity in fishery science. U.S. Dept. Int., Fish and Wildl. Serv., Spec. Sci. Rept.: Fisheries No.127:1-55.

HOLMES, HARLAN B. 1948. History, development, and problems of electric fish screen. U.S. Dept. Int., Fish and Wildl. Serv., Spec. Sci. Rept.: Fisheries No.53:1-62.

MCLAIN, ALBERTON L. AND WILLIS L. NIELSEN. 1953. Directing the movement of fish with electricity. U.S. Dept. Int., Fish and Wildl. Serv., Spec. Sci. Rept.: Fisheries No.93:1-24.

SELECTED REFERENCES

ABE, NOBORU. 1935. Galvanotropism of the catfish: *Parsiluris asotus* (Linne). Tohoku Imperial Univ. (Sendai, Japan), Sci. Repts. Fourth Series (Biology), 9(4):393-406. (Biol. Abstr. 5573, 1936).

ARIEFF, ALEX J. 1948. Threshold studies in electrical convulsions using a square wave stimulator. Northwestern Univ. Med. Sch., Quart. Bull., 22(1):10-16.

BEST, CHARLES H. AND NORMAN B. TAYLOR. 1950. The physiological basis of medical practice. Williams and Wilkins, Baltimore, pp.906-907.

BOWMAN, H. P. 1928. Chronaxie of fish muscle. Arch. Néerl. Physiol., 12:403-415.

BURNET, A. M. R. 1952. The design and use of an electric fishing machine. Austral. J. Marine and Fresh-water Res., 3(2):111-125.

DUKES, H. H. 1947. The physiology of domestic animals. Comstock Publishing Co., Ithaca, N.Y. 817pp.

HASKELL, DAVID C. 1940. Electric shock provides method of anesthetizing fish in laboratory. Progr. Fish Cult., 49:33-34.

———, JOHN MACDOUGAL, AND DONALD GEDULDIG. 1954. Reactions and motion of fish in a direct current electric field. N.Y. Fish and Game J., 1(1):47-74.

HAUCK, FORREST R. 1949. Some harmful effects of the electric shocker on large rainbow trout. Trans. Amer. Fish. Soc., 77(1947):61-64.

MAREAU, LOUIS, MARVIN BALISTOCKY, AND L. V. HEILBRUNN. 1948. Shock due to electrical injury in frogs. Amer. J. Physiol., 154:38.

MEYER, W. H. F. 1927. Contraction rates in fish muscles. Arch. Néerl. Physiol., 12:162-187.

PROSSER, C. L. (editor); D. W. BISHOP, F. A. BROWN, JR., T. L. JAHN, C. L. PROSSER, AND V. J. WULFF. 1950. Comparative animal physiology. W. B. Saunders Co., Phila. 888pp.

TRAUTMANN, ALFRED AND JOSEF FIEBIGER. 1952. The histology of domestic animals. Comstock Publishing Co., Ithaca, N.Y. 426pp.

Received for publication December 6, 1956.

NICOTINE SALICYLATE FOR CAPTURING DEER[1]

Jack A. Crockford,[2] Frank A. Hayes,[3] James H. Jenkins,[4] and Seldon D. Feurt[5]

The Georgia Game and Fish Commission, Atlanta, and The University of Georgia, Athens

Since the turn of the century the need for an expeditious and simplified method of capturing wild animals has been recognized. Although various trapping and corralling procedures have been successfully employed in many locales and circumstances, the potentialities of a drugged dart have warranted considerable speculation (Bartlett, 1933).

The use of poisonous arrows for immobilizing and killing animals—including man—has long been an intriguing source of material for popular writers (Krukoff and Smith, 1937). Within recent years similar methods for the capture and restoration of wild animals have been under investigation (Hall, *et al.*, 1953; Goetz and Budtz-Olsen, 1955; and Jenkins, *et al.*, 1955). These studies have been continued, and it is the objective of this paper to offer a preliminary report on an effective and practical means of catching the white-tailed deer (*Odocoileus virginianus*).

Extensive experimental work directed toward this end was commenced in early 1955, and the curare alkaloids and synthetic curare-like compounds appeared to be in order for continued study. During this phase of the project, only one wild deer was successfully taken with flaxedil (Lederle Laboratories Division, American Cyanamid Co., Pearl River, New York), and this group of compounds was found to have many undesirable characteristics; further work with similar-acting drugs was discontinued. In a subsequent effort toward arbitrarily selecting a drug, the strychnine salts were evaluated. Although 21 animals were taken with these compounds, the mortality rate was most discouraging (Jenkins, *et al.*, 1955).

[1]These studies have been supported by the Georgia Game and Fish Commission and the University of Georgia.

[2]Federal Aid Coordinator, Georgia Game and Fish Commission.

[3]Assistant Professor, Department of Pathology and Parasitology, School of Veterinary Medicine, University of Georgia.

[4]Assistant Professor, Wildlife Management, School of Forestry, University of Georgia.

[5]Associate Professor, Department of Pharmacology and Pharmacognosy, School of Pharmacy, University of Georgia.

It was concluded that the ideal drug for these purposes must possess the following characteristics: (a) effective dose not to exceed the quantity that can be carried on an appropriate-sized dart; (b) stability; (c) rapid absorption into the systemic circulation; (d) rapid onset of action resulting in sufficient immobilization of the subject; (e) a wide margin of safety (3X minimum); (f) no antidote required; (g) rapid elimination from circulatory system; (h) no drastic effect on gestation; and (i) no permanent damage to an animal.

After screening numerous compounds by subcutaneous and intramuscular injections into goats, nicotine salicylate was selected for extensive trials.

PHARMACOLOGICAL ACTION OF NICOTINE

Tobacco (*Nicotiana Tabacum*) and its active constituent, nicotine, have had little if any rational therapeutic application other than psychotherapy and as a pesticide. The pharmacodynamics of nicotine have been the subject of intensive investigation since Langley and Dickinson (1889) demonstrated that topical application could produce ganglionic paralysis.

The term *nicotine action* of autonomic active drugs refers to an evanescent stimulation followed by ganglionic paralysis; this typical biphasic action is present at all autonomic ganglia, myoneural junctions and affects the central nervous system, varying in duration and intensity as a function of dose, mode of administration and species of animal. The flaccid paralysis characterized in man and many other animals after nicotine intoxication has resulted in the alkaloid being classified pharmacologically with curare or as possessing a curariform action (Salter, 1952).

MATERIALS AND METHODS

The Instrument of Delivery

Although various modes of propulsive delivery of a drug have been described (Hall, *et al.*, 1953; Goetz and Budtz-Olsen, 1955; and Jenkins, *et al.*, 1955), continued work toward perfecting an instrument of this kind was most essential to the project.

Air guns were used, being conversions of the Crossman models 100, 101, or 102 (Crossman Arms Company, Rochester, New York). This conversion consisted of rebarreling with seamless steel tubing, fitted in the same manner as the factory barrel. The tubing was of the following dimensions: 0.440-inch O.D., 0.307-inch I.D. and 20 1/4 inches long. In order that the bolt could be completely withdrawn for loading, the bolt stop was removed. This accommodated the dart, which was inserted from the rear. The pellet seating shaft on the fore end of the bolt was discarded and a 1 3/8-inch piece of 1/16-inch piano wire was silver soldered in its place. The dart skirt was thus seated forward of the air intake in the breech. These guns were then fitted with good-quality low-power telescopic sights with coarse posts or dot reticuli to facilitate accurate night shooting.

The darts were composed of low-carbon drill-bit shanks with points made from steel tubing. The shanks were sealed into plastic bases to which were cemented cotton-cord

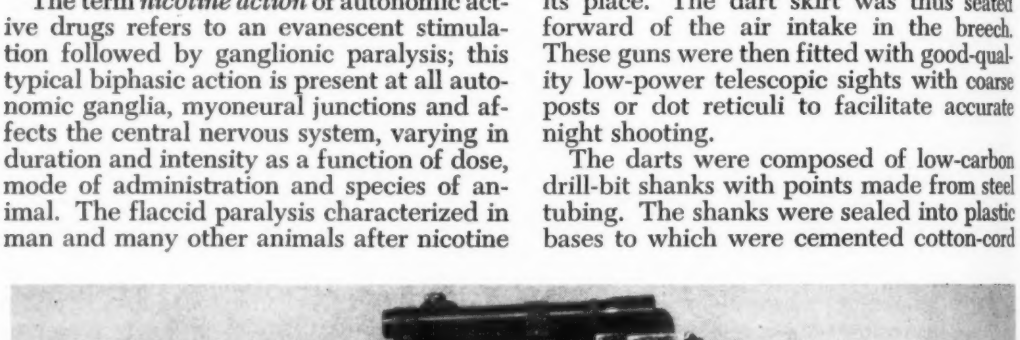


FIG. 1. Modified Crossman air-gun. Beneath gun—from top to bottom—is shown a sealed calcium chloride tube containing a dart, a loaded dart and an "empty" dart.

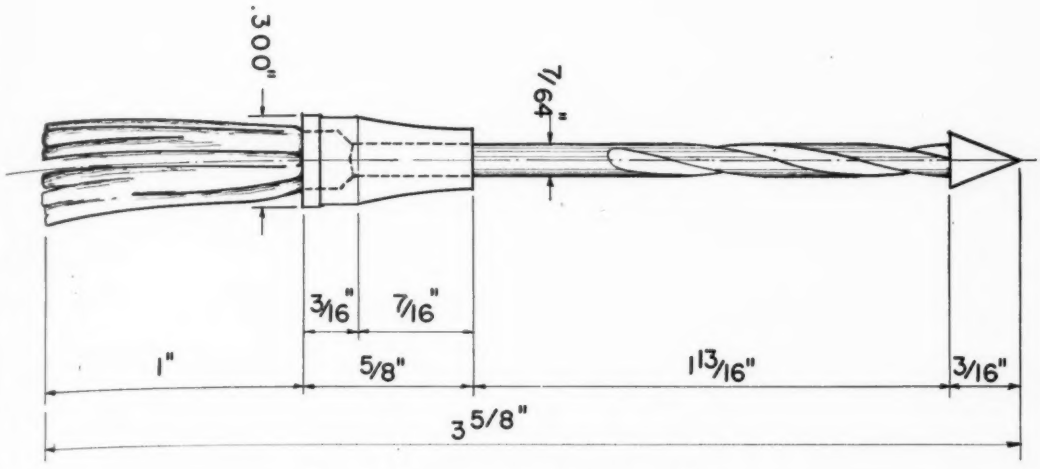


FIG. 2. Diagram of dart drawn to scale.

skirts. These darts were fabricated in the following manner. Sections 5/8 inch long were cut from 3/8-inch methyl methacrylate rod and drilled longitudinally to shank diameter, 7/64 inch. The drill shanks (2 1/2 inches in length) were then roughened on a coarse grinding wheel for approximately 1/2 inch at one end and mechanically bonded by heat to 7/16-inch depth in the plastic-base sections. Recesses in the plastic bases were then drilled from the rear, 3/16 inch in diameter, to the depth of the dart shafts (approximately 3/16 inch) and turned to shape and diameter in a metal turning lathe. Points were made from 3/16-inch sections of steel tubing, 3/16-inch O.D. and 7/64-inch I.D. These sections were soft soldered on the bits 3/32 inch from the tips and ground to a conical shape. The 1-inch skirts, consisting of 8 strands of No. 24 white cotton twine, were attached with plastic cement in the 3/16-inch holes in the bases. The skirts were painted with codit reflective liquid (Minnesota Mining and Manufacturing Company, St. Paul, Minnesota), which permitted observation at long range in the operator's light.

Method of Applying Drug to Dart

Powdered nicotine salicylate was massed by the addition of purified honey in sufficient quantity to form an adhesive, pliable material. This adhesive substance was applied to the shaft of the dart and formed to the desired diameter. The loaded darts were placed in tightly closed tubes containing granular calcium chloride to dehydrate and partially harden the compound; dehydration required approximately 24 hours. Upon removal of darts from calcium chloride the hygroscopic nature of the alkaloidal salt converted it back into the readily absorbable state.

Hunting Procedure

Many factors entered into the successful field application of this technique. Most of the work with deer was carried out on Ossabaw Island, Georgia; therefore, the described approach to hunting is at present limited to this or similar ecological areas.

In order to obtain ample shots and follow the subjects successfully, work was confined to night hunting ("jack-lighting"). Where possible, the spotlighting was done from a small truck. When an animal was located, the "gunman," preferably alone, made the stalk on foot as rapidly but silently as possible, with discreet use of the spotlight. The shot was made into the hind quarters and preferably in the gluteus medius, biceps femoris, semitendinosus or semimembranosus muscles.

Immediately after a shot, the operator visually confirmed the hit, and if dart penetration was obtained, a red spotlight (Southern, 1955) replaced the previous white "jacklight." The hunter then moved only enough to keep the animal in sight. If the observer temporarily lost sight of the animal, a return to the white light often aided in relocating the subject. If visual contact

TABLE 1. — DEER CAPTURED WITH NICOTINE SALICYLATE DARTS

Deer No.[1]	Date of Capture	Sex	Body Wt. in Lbs.	Dart Load in Mgm.	Mgm./Lb. Body Wt.	Place of Hit[2]	Minutes Required For Inactivation	Minutes Required Before Apparent Recovery	Effect of Nicotine Salicylate
1-P	4-13-56	M	40	200	5.0	I.M.	2.5	34	Brief period of excitement followed by partial paralysis.
2-W	4-14-56	F	75	200	2.7	I.P.	7.0	20	Became very un-coordinated with marked staggering. Ran 100 yards before capture.
3-W	4-15-56	M	57	200	3.5	I.M.	3.0	15	Brief period of excitement then down fast in state of partial paralysis.
4-W	4-15-56	M	85	200	2.4	S.Q.	15.0	25	Standing when approached. Near complete catalepsy. Caught by rear legs.
5-W	4-16-56	F	75	200	2.7	I.M.	5.0	20	Brief period of excitement followed by partial paralysis. Down fast.
6-W	4-16-56	F	88	200	2.3	I.M.	?	5	Lost 2 min. after hit. Found 30 min. later in a poorly co-ordinated condition. Caught animal after 200-yard chase.
7-W	4-17-56	F	45	200	4.4	I.M.	2.5	14	Brief period of excitement then down fast.
8-W	4-17-56	F	60	200	3.3	I.M.	5.0	8	Brief period of excitement without marked paralysis. Down in excitement.
9-W	6-3-56	M	136	300	2.2	I.M.	3.0	40	Down fast in state of partial paralysis.
10-W	6-4-56	F	70	300	4.3	I.M.	3.5	45	Brief period of excitement then down fast in partial paralysis.
11-W	6-5-56	F	80	300	3.8	I.M.	3.0	45	Down fast in state of partial paralysis.
12-W	6-5-56	F	80	300	3.8	I.M.	2.5	40	Brief period of excitement then down fast in partial paralysis.
13-P	7-11-56	M	115	300	2.6	I.M.	4.0	45	Total catalepsy. Later went down in state of partial paralysis.
14-P	7-11-56	M	105	300	2.8	I.M.	5.0	30	Brief period of excitement. Ran for 50 yards then fell in a paralytic condition.
15-W	7-25-56	M	85	300	3.6	I.M.	3.5	60	Brief period of excitement. Ran for approximately 10 yards. Down fast with progressive paralysis.

(Continued on next page)

TABLE 1. — Continued

Deer No.[1]	Date of Capture	Sex	Body Wt. in Lbs.	Dart Load in Mgm.	Mgm./Lb. Body Wt.	Place of Hit[2]	Minutes Required For Inactivation	Minutes Required Before Apparent Recovery	Effect of Nicotine Salicylate
16-W	7-26-56	F	70	300	?	I.M. I.M.	24.0	15	Observed animal for 8 min. after first hit. Partial catalepsy but could still run. Lost animal but found 20 min. after initial hit. Shot second time after which animal fell in 4 min. Brief period of excitement followed by slight paralysis.[3]
17-W	7-26-56	M	105	300	?	I.M. I.M. I.M.	48.0	90	Observed animal for 6 min. after first hit. Few symptoms. Lost animal but found 18 min. after initial hit. Shot second time, after which the animal fell in 5 min. Escaped but relocated 45 min. after first hit. Shot third time after which inactivation was complete in 3 min, Down fast in brief period of excitement; followed by paralysis.[3]

[1] P for penned deer; W for wild deer.
[2] I.M. indicates intramuscular hit;
I.P. indicates intraperitoneal hit; and
S.Q. indicates subcutaneous hit.
[3] Inferior quality of drug responsible for the necessity of additional shot(s) and subsequent delay in capture.

was not established, the operator exercised judgment in moving into a position where the animal might be expected to become immobilized. After eight minutes following a confirmed "good hit," if the animal was not under surveillance, the remainder of the hunting party was called in for a search.

RESULTS

Nicotine salicylate, delivered in the described manner, was tested on 21 experimental, penned goats. The effective dosage was established on these animals and was found to approximate 200-300 mgm. for adults weighing from 80 to 90 lbs. This "dart load" was also shown to be effective on goats weighing up to 120 lbs. and at the same time was safe for animals weighing as little as 50 lbs.

Although goats were immobilized in over 100 trials with nicotine and its salts, there was not a single fatality. Several experimental goats were completely inactivated with nicotine as many as six times. These animals were observed for as long as five months, and no adverse effects from the drug became apparent. These encouraging facts, at least in part, also applied to 17 deer captured with the drug (Table 1).

Animals #1, #13, and #14 were penned deer that were kept in a 5-acre enclosure where daily observations were possible. Deer #1 has been observed for at least four months following its inactivation with nicotine salicylate; animals #13 and #14 have been observed at least one month since they were drugged. From all outward appearances, these subjects have experienced no ill effects from the procedure.

Animals #2, #3, #4, #6, and #7 were wild deer taken as described and moved to the same enclosure. Number 2, #6 and #7

FIG. 3. (Deer #13) Complete catalepsy in animal that received 300 mgm. of nicotine salicylate.

were does taken during late gestation. Approximately four months from the date of capture, two of these three does were nursing fawns. The other doe (#6) died two weeks after arrival at the pen. This animal was lost shortly after shooting, and when finally located 30 minutes later, the maximum effective level of the drug had been excreted. A chase of approximately 200 yards was necessary for capture, which was made rather roughly. It is thought that injury to the pregnant animal was inflicted at this time. The remainder of this group of animals appeared to be in excellent condition four months after capture. Deer #5 and #8 escaped because handling facilities were not immediately available.

Deer #9, #10, #11, #12, #15, #16, and #17 were caught with varying degrees of efficiency, handled until adequate recovery had been attained, and released in the vicinity of capture. These hunts were conducted during the season of late gestation or early lactation and antler development; both situations rendered transportation procedures undesirable for the animals. The major objective of the hunts was for demonstration.

RECOMMENDATIONS AND COMMENTS

Although adequate testing with nicotine salicylate has not been completed, the following recommendations and comments appear to be in order and have become a part of the standard operative procedure.

a. The point or the "head" of a dart should be slightly greater in diameter than that of the drug load. This prevents shearing of the drug and also facilitates skin penetration.
b. If a loaded dart is removed from the calcium chloride tube and is not used within a period of six hours, it should be returned to the original container. Here it will again dehydrate and retain its effectiveness.
c. The Crossman air gun used for this work is best shot with four or five pumps in the compression chamber. The maximum effective range for this instrument is about 25 yards. Long and uncertain shots should be avoided.
d. Three hundred milligrams of nicotine salicylate are recommended as the efficient and safe dose for the white-tailed deer in this region.
e. A good intramuscular hit is absolutely essential for the desired results. Intraperitoneal or subcutaneous injection greatly reduces the speed of absorption of the drug, and at the prescribed dosage, excretion often exceeds absorption, and adequate immobility may not occur. The desired effect should take place within approximately three to five minutes.
f. A transitory period of excitement usually precedes paralysis. The excitatory phase lasts approximately a minute, and the

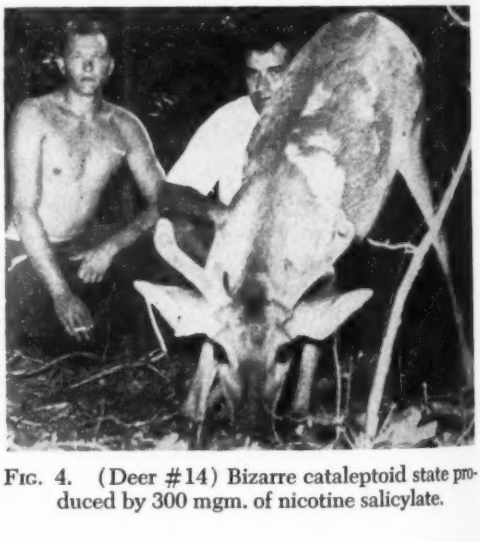


FIG. 4. (Deer #14) Bizarre cataleptoid state produced by 300 mgm. of nicotine salicylate.

FIG. 5. (Deer #11) Examination of animal in curariform stage.

curariform stage may persist for as long as an hour. Considerable salivation often occurs; however, this is no cause for great concern. Caution should be exercised that the tongue is protruding and that the nostrils are not obstructed. Holding the animal's head slightly above the horizontal plane appears to "comfort" the patient. Within a short time the reflexes of the neck musculature will return and the latter procedure is no longer indicated.

g. Occasionally the drugged deer assumes a state of catalepsy, thus allowing its body to be molded into bizarre positions comparable to those described in the classic experiments with bulbocapnine (Amadon and Craige, 1936). This indicates a low systemic level of the drug, and rapid recovery may be anticipated. An animal in this state is usually found in a standing position and is easily caught. This cataleptic phenomenon occurs in about 15 to 20 per cent of drugged goats and deer; some experience is required to detect the syndrome.

h. Infrequently a vein or artery is severed by the dart. Although no dangerous loss of blood has been encountered in these mishaps, an injectable coagulant appears to be indicated in controlling hemorrhage.

i. Both cardiac activity and respiratory efforts of nicotine-drugged animals have been improved by the intramuscular injection of amphetamine salts. In working with goats and deer, however, this procedure has never been deemed essential. Extreme caution should be observed in using this drug.

j. As a precautionary measure against infection possibly introduced by the dart, 1 to 2 million units of penicillin are routinely administered to the patient.

k. As further precaution in an area where screwworms (*Callitroga americana*) are prevalent, it is recommended that the dart-inflicted wound be covered with a reliable fly-repellent preparation.

l. For restraint purposes, pentobarbital sodium has been found to be both advantageous and safe, even though used in conjunction with nicotine. The recommended dose is 5 cc. (64 mgm./cc.) per 100 lb. body weight, administered intrathoracically. This makes handling of the animal relatively simple for at least an hour, and at the same time much strain on both the operators and captive deer is avoided.

m. It appears that different supplies of nicotine salicylate may show considerable variation in activity or "strength." Each lot number of the drug procured should be biologically assayed before its use in field work. Goats are ideal experimental animals for testing the quality of nicotine salicylate, and their response to the drug is identical with that of deer.

n. Nicotine has been described as "one of the most toxic of all drugs and acts with a rapidity comparable to that of cyanide." The lethal oral dose of the alkaloid for man is generally considered to be in the neighborhood of 60 milligrams, with death resulting from respiratory suppression and myocardial atonia (Goodman and Gilman, 1955). Caution should be observed in handling this drug.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the cooperation of Mr. and Mrs. William F. Torrey. Without their interest and concern for wildlife conservation, this excellent "35,000-acre laboratory" (Ossabaw Island) would not have been available for these studies.

The authors also wish to thank Robert W. Cannon (project leader, W-14-D Refuge Management, Georgia Game and Fish Commission) and Johnny L. Jernigan (senior student in wildlife management, School of Forestry, University of Georgia) for their invaluable assistance and continued interest in this project.

SUMMARY

Nine factors have been listed as essential characteristics of a drug to be used in capturing deer with a "dart-gun technique." Nicotine salicylate appears to possess these qualities. An efficient means of delivering the compound has also been described. Additional items of pertinent importance have been included for consideration.

LITERATURE CITED

AMADON, R. S. AND A. H. CRAIGE. 1936. Observations on the use of bulbocapnine as a soporific in horses. J. Amer. Vet. Med. Ass., 88:737-754.

BARTLETT, I. H. 1933. A report of conditions among the deer herds of Alpena Co. Special Report (mimeo.), Game Div., Mich. Dept. Conserv., Lansing.

GOETZ, R. H. AND O. BUDTZ-OLSEN. 1955. The circulation of the giraffe. S. Afr. Med. J., 29:773-776.

GOODMAN, L. S. AND A. GILMAN. 1955. The pharmacological basis of therapeutics. Ed. 2. The Macmillan Company, New York, N.Y. xiii + 1831pp.

HALL, T. C., E. B. TAFT, W. H. BAKER, AND J. C. AUB. 1953. A preliminary report on the use of flaxedil to produce paralysis in the white-tailed deer. J. Wildl. Mgmt., 17:516-520.

JENKINS, J. H., S. D. FEURT, F. A. HAYES, AND J. A. CROCKFORD. 1955. A preliminary report on the use of drugs for capturing deer. Proc. S.E. Assoc. Game and Fish Comm., 2:41-43.

KRUKOFF, B. A. AND A. C. SMITH. 1937. Notes on the botanical components of curare. Bull. Torrey Bot. Club., 64:401-409.

LANGLEY, J. N. AND W. L. DICKINSON. 1889. On the local paralysis of peripheral ganglia, and on the connexion of different classes of nerve fibers with them. Proc. Roy. Soc., 46:423-431.

SALTER, W. T. 1952. A textbook of pharmacology; principles and application of pharmacology to the practice of medicine. W. B. Saunders Co., Philadelphia, Pa. xiii + 1240pp.

SOUTHERN, H. N. 1955. Nocturnal animals. Sci. Amer., 193:88-98.

Received for publication July 16, 1956.

A BRIEF ACCOUNT OF THE DEER IN AUSTRALIA

Arthur Bentley

Malvern, Victoria, Australia

No species of deer is indigenous to Australia, Tasmania, or any of the adjoining islands. The deer now established there were introduced during the nineteenth and twentieth centuries. No comprehensive record of their introduction, subsequent liberation, and present range exists. Little attention has been paid to the deer by naturalists recording the wildlife of Australia.

A number of factors contribute to this neglect. The foremost is that deer are not native to the country and therefore are lumped together with rabbit, hare, and fox under the heading of "introduced fauna" and classed as a pest. Supporting this official and quite general view is the wide recognition of the rather unique place held in the order of things by the native fauna. The Fisheries and Game Departments of the various states are, generally speaking, little concerned with the introduced species; the deer are not recognized as the magnificent game animals that they are, and consequently their control and management receives next to no attention.

Often deer were turned out in secret—a precaution taken to prevent valuable game from being destroyed by irresponsibles before it had sufficient time to become established. Because the acclimatisation movement was at its height at a time just beyond the range of present living memory, and because few records were kept, knowledge of many of the attempts to introduce game to Australia are lost to us. It is therefore difficult to collect the information necessary for a complete survey of deer in this area. The greater part of the work remains to be done.

Methods and Materials

Since 1937, but excluding the war years, deer in Australia have been my major leisure-time interest, and the bulk of the information in the present paper is the result of my own observation and inquiry. The present paper is a summary of a mass of detail that I have gathered during these years. My initial knowledge of the acclimatisation scheme and early shipments of deer came from the study of the Reports of the Royal Victorian Acclimatisation Society, 1870-74, from Edward Wilson's pamphlet *Acclimatisation* (Unwin, London, 1875), and from a seemingly endless search in the files of the Melbourne newspaper, *The Argus*, from about 1860 forward.

My next step was to duplicate a questionnaire that I posted to police officers, school principals, and to Lands Department and Forestry officers in districts where deer had been turned out or were rumoured to be. With the help of information supplied by these people, I was able to get in touch with individual persons who had local deer information. Sometimes I was fortunate and found persons whose parents or grandparents were responsible for having imported or liberated the deer. I also used the press and radio to find further sources of information. Finally, I made personal inquiry at, and sometimes hunted, practically all localities mentioned in the present paper, except those in Western Australia, Tasmania and Northern Territory.

The Acclimatisation Scheme

In the latter half of the nineteenth century, the interest in transplanting animals, birds, and plants from one country to another was world-wide. Acclimatisation societies were formed in many countries with a view to the wider distribution of useful species.

In Australia, after the economy of the early settlements was secure, many of the more well-to-do colonists sought for their pleasure to introduce certain game animals and birds from the Northern Hemisphere. Many settlers, too, longed for the familiar sights and sounds of the faraway lanes and hedgerows of their native land. So, besides the shipments of deer, foxes, rabbits, and hares, came consignments of blackbirds, thrushes, linnets, skylarks, sparrows, and other common British birds to the new land in the south.

It was not long before individual effort along these lines became organized, for the

idea had many influential supporters. Foremost among these was Edward Wilson, philanthropist and one-time owner of the Melbourne newspaper *The Argus*. It was at a public meeting convened by this gentleman in 1861 that the Victorian Acclimatisation Society was formed. Edward Wilson continued his work throughout Australia, and eventually all the states had their own societies. These groups received support from the government by grants of land and money, and there developed a flourishing exchange and sale of fauna. Ships' captains, at government instigation, were instructed by the owners to offer every facility to persons and organizations shipping livestock between countries. Some lines serving Australian ports carried fauna free of charge.

Between 1860 and 1880 occurred the peak of importations of deer. After 1880, shipments declined and no record has been found of an importation between 1910 and the present time.

As most liberations of deer were made in Victoria, New South Wales, South Australia, and Queensland, it follows that the greatest concentrations occur in the timbered ranges of eastern and southeastern Australia.

SPECIES OF DEER INTRODUCED

RED DEER (*Cervus elaphus*).—The red deer in Australia are descendants of animals from Windsor Great Park and Knowsley Park, England. The original animals were, in many cases, presented to the acclimatisation societies by the late Queen Victoria. The finest herd to be raised from a nucleus of Windsor Park deer was that established at Werribee Park, Victoria, by the late Thomas Chirnside. Deer from this herd roamed the rich plains of western Victoria around the turn of the century. Closer settlement of the area has since driven the deer into the cover of the ranges. Deer from Werribee Park were distributed to other owners of large properties in the Western District, and stags were shipped to New Zealand in an attempt to improve the Otago herd there.

Knowsley Park deer were imported by the Melbourne Hunt Club to form a herd to be used for stag hunting. It has not been possible to trace the fate of all these animals, but there is little doubt that Victoria's present red deer population owes something to the Hunt Club.

The species is plentiful in Queensland in the mountainous country at the head of the Brisbane River. In 1915, the Queensland government liberated a number of red deer on Hinchinbrook Island off the coast. The animals were intended to be a source of food for any persons unfortunate enough to be shipwrecked on Hinchinbrook. This large island is mountainous and covered by dense tropical vegetation. As it is uninhabited and visited only by prospectors and occasional fishermen, it is not definitely known if deer still survive on the island. There is evidence to suggest that the deer have crossed to the mainland—this entailing a swim of one or one and one-half miles at the narrowest part of the strait.

In South Australia, red deer were once numerous in the southeastern part of the state. Their origin is somewhat obscure, and it is thought by some residents of the locality that they migrated from the Western District of Victoria. This suggestion is not improbable, but it is more likely that the deer are descendants of animals sent from the Werribee Park herd to some of the larger stations in this part of South Australia. The red deer in the southeastern part of this state are steadily decreasing, and there may have been some movement westward. This is supported by a reliable report that a herd of about 12 red deer was seen some miles northwest of Lake Bonney. Here there is a vast area where the species could easily become established.

At least two concentrations of red deer occur in New South Wales. The first of these is located in and about the national park south of Sydney. Although red deer are often blamed for damage to crops and gardens in this area, fallow deer predominate there. To date it has not been possible to define accurately the range limits of the national park deer; there appears to be a definite spread toward the south.

The second concentration of this species in New South Wales is located in the southeastern part of the state near the Victorian border in the area known as the Quidong. The deer are descendants of a number that were kept in enclosures on a station property near Bombala before the 1914-18 war. Occasionally, deer escaped from the enclosures and in 1918, when the property was sold, the deer were liberated into the bush. They appeared to thrive, and groups of up to ten

animals have been sighted. There are indications that the deer have penetrated into Victoria and are moving south down the Bemm and Brodribb rivers.

Red deer from Werribee Park, Victoria, were sent to West Australia and turned out near Pinjarra where they quickly became established. In recent years little has been heard of them. It does seem certain that they still exist in the waste land toward the coast from Pinjarra, but nothing is known of their numbers. Certainly they are not nearly so numerous near Pinjarra as formerly. A possible explanation for their decrease may lie in the presence in this area of the zamia palm (*Macrozamia fraseri*), a poisonous plant that causes partial paralysis of animals that feed on it. Cattle will survive for several years when so afflicted, but the effects on deer may be more severe.

FALLOW DEER (*Dama dama*).—Fallow deer are widespread in the eastern midlands of Tasmania. Their main range can be defined by a line drawn from Campbell Town to Evandale, Lake Leake, Swansea, and Ross. However, they do occur outside this area. The herds originated from English importations about 1850. They were intended for hunting, and during the hunts bucks escaped into the bush. Subsequently, does were liberated intentionally so that the species would become established in a wild state. Shipments of fallow deer were sent to other parts of Australia from Tasmania. At least one consignment was sent to the South Island of New Zealand for liberation at Culverden.

Until the winter of 1953 it was thought that the fallow deer, which were once plentiful in the hills about Adelaide, South Australia, were shot out. In that winter, however, a small group was sighted north of the city. By far the largest concentration is located in the pine forests and scrub country within the general boundary of a triangle formed by a line from Mount Gambier to Millicent and Naracoorte. Another large herd is running on private property near Two Wells, having been first liberated in this locality in 1917.

In Victoria the species is limited to three comparatively small areas. The first is in the ranges about Healesville in east-central Victoria. The second is a small "overflow" herd from New South Wales and is located west of Albury on the Murray River. The third is a penetration from southeastern South Australia into the country near Casterton.

Four localities in New South Wales hold fallow deer: (1) the country along the eastern bank of Lake George, (2) the national park in New South Wales, (3) the hills east of Albury along the northern bank of the Murray River, and (4) the New England ranges about Glen Innes, where six deer were first liberated in 1926, and 300 were counted a few years ago during a severe winter. Reports of individual animals from the Monaro Plains in southern New South Wales may indicate the location of another herd or herds there.

In Queensland, fallow deer are well established near Toowoomba. In 1916, along with the sambar and barasingha deer, 50 fallow deer were released on the Coburg Peninsula in the Northern Territory. There are recent and reliable reports of deer on the peninsula, but no description accompanies them. This is another area from which detailed reports are exceedingly difficult to obtain. Three or four liberations of fallow deer were made at Cape Leeuwin, West Australia, in the last century. About the time of the 1914-18 war the Acclimatisation Society reported that they were thriving.

SAMBAR DEER (*Cervus unicolor*).—In Australia the stronghold of this big deer is Victoria. The greatest numbers are to be found in the Gippsland forest in eastern Victoria. There are also two localities in the western part of the state where they occur—in the Grampians and in the timbered country at Mount Cole. They are also plentiful on French Island off the southern coast. This species was also released in West Australia, in New South Wales in the national park, and on the Coburg Peninsula in the Northern Territory. Only from the last-named locality have animals fitting the sambar's description been recently reported.

MOLUCCAN RUSA (*Cervus timorensis moluccensis*).—In 1910 this variety of deer was liberated on Friday Island off Cape York Peninsula, North Queensland. They did remarkably well and spread to adjoining Prince of Wales Island, swimming about three-quarters of a mile in shark- and crocodile-infested water to do so. Both islands are now well stocked. Around 1914 a number of

these deer were taken from Friday Island and turned out on Possession Island, some miles away, where they are still established. Between Possession Island and the mainland are a number of islands that may form a convenient line of migration to the mainland. A deer was once seen swimming in the sea near these islands by the crew of a small ship. Sambar and rusa were turned out in the same area in Gippsland, Victoria, and it is possible that they have crossbred. Although a few rusa are shot in this area, they are becoming quite rare. Rusa were also liberated in the New South Wales national park, and they are still established there.

HOG DEER (*Axis porcinus*).—This species is well established in many localities in southeastern Victoria. It prefers the grassy coastal flats and has not penetrated far into the foothills. Hog deer are also numerous on some of the islands off the southeastern coast. An unconfirmed report locates the species in a locality near Holbrook in New South Wales (approximately 50 miles north of Albury).

AXIS DEER or CHITAL (*Axis axis*).—To date only two herds of axis deer have been located. One herd, the larger of the two, is near Charters Towers in Queensland. It was established about 1866 by the introduction of a stag and two hinds by William Hann. The other herd is located in the Grampians, a mountain range in western Victoria. The size of this herd is not known, but individuals from it are seen frequently. They are not hunted, as the area is a sanctuary.

BARASINGHA (*Cervus duvaucelii*) and JAPANESE SIKA (*C. nippon*).—Both of these species were liberated in Australia in the last century, and a few years later they were reported to be doing well. In southern Gippsland the writer has seen deer that closely resemble the sika. It is not unlikely that both species are established somewhere in Australia.

ECOLOGICAL NOTES

Natural Enemies of the Deer in Australia.—These are very few. Wild dogs, a term that includes the dingo (*Canis dingo*), may be the most important, although it is difficult to appraise their exact effect on deer populations. In eastern Victoria, as close as 50 miles from Melbourne, there are many wild dogs. These are domestic dogs "gone bush" with an odd dingo here and there among them. They may account for a few sambar calves; but wallabies, kangaroos, and other native animals would be their staple food. Dingos do prey on the herd of axis deer located near Charters Towers in Queensland. Crocodiles (*Crocodylus porosus*) will undoubtedly take a few of the rusa on Friday and Prince of Wales islands. It is possible that bush fires would destroy a number of deer in some localities. Deer in Queensland are frequently infested by cattle ticks and have been noted to be in poor condition.

Food Plants.—In Australia the deer population is not large and only makes itself felt in isolated localities. Complaints of deer damage come mainly from potato growers and orchardists. No timber trees are damaged by them in southeastern Australia, as the native eucalypts are unpalatable to deer. There is a wide variety of native plants that are plentiful and favored by the deer, including two or three kinds of ferns, several native grasses, and a number of shrubs. There is an abundance of food, and a "poor" deer is never seen, except in the tick-infested country of Queensland.

TABLE 1. — HUNTING TAKE BY ONE HOUND PACK IN GIPPSLAND[1]

Year	Months Hunted	Number of Sambar Deer Taken			
		Stags	Hinds	Sex Unknown	Total
1954	March to December	23	18	3	44
1955	January to December	33	24	1	58
1956	January to September	15	14	3	32
Totals taken		71	56	7	134
Per cent by sex		56	44	—	100

[1] Owned by S. A. Ashford of Gembrook, to whom the author is much indebted for his cooperation in this study.

TABLE 2.—REPRODUCTIVE CLASSIFICATION OF SOME SAMBAR DEER KILLED IN VICTORIA SINCE 1950[1]

	Months												
	1	2	3	4	5	6	7	8	9	10	11	12	Total
Number of stags killed	9	2	9	11	9	12	15	10	5	3	3	5	93
Antler development													
None	–	1	–	–	–	–	–	1	–	2	1	–	5
Under one-half	2	1	1	6	–	3	–	–	–	–	–	2	15
Over one-half	1	–	7	4	3	3	2	–	–	–	–	1	21
Complete[2]	6	–	1	1	6	6	13	9	5	1	2	2	52
Number of hinds killed	1	2	5	8	9	17	15	12	2	2	4	3	80
Fetal development													
None	–	–	–	3	1	3	4	5	1	1	–	–	18
Less than half	–	–	–	1	1	2	1	–	–	–	3	–	8
Half to full	1	–	3	2	5	7	3	3	–	–	1	2	27
Young calves	–	2	2	2	2	5	7	4	1	1	–	1	27
Total both sexes	10	4	14	19	18	29	30	22	7	5	7	8	173

[1] Includes animals shown in Table 1.
[2] Antlers fully developed, hard and clean.

Hunting.—Of all deer concentrations in Australia, there is little doubt that the sambar and the hog deer in Gippsland sustain the heaviest hunting pressure. They have been legally hunted for upwards of 30 years without regard for sex or season. It is the opinion of hunters of long experience that there are as many sambar in Gippsland today as at any time previously but that they are much more widespread.

The much-hunted hog deer has also increased its range, to the east along the coastal flats. Its numbers are sustained by a natural movement from the Wilson's Promontory National Park and possibly from one or two close-lying islands which are also sanctuary for this species.

Elsewhere in Australia, with the possible exception of Tasmania, hunters' toll would have no pronounced effect on the deer population under conditions prevailing at the time of my writing (1956).

In Victoria the best deer country is heavily timbered, steep, and has thick undergrowth. Because of this, hounds are used to hunt deer. They are usually foxhounds or bloodhound–foxhound crosses; and they are, of course, followed on foot. It is a strenuous sport. In other states of Australia, deer are walked-up or still-hunted. The number of sambar taken by one pack of five hounds in Gippsland is shown in Table 1. There are probably 12 to 15 similar packs hunting in Gippsland but not all with such success. Most hunting is carried on during the cooler months of March to October. In one sample that I studied (Table 2), 55 per cent of the stags taken possessed fully developed antlers and 64 per cent of the hinds had calves or fetuses.

SUMMARY

The peak of importations of deer in Australia took place between 1860 and 1880, the last of record being before 1910. Red deer are plentiful in mountainous terrain at the head of the Brisbane River, are decreasing in South Australia and West Australia, and occur in two concentrations in New South Wales. Fallow deer are well established in Tasmania and in Queensland, hog deer and sambar deer mainly in Victoria, and rusa deer mostly on islands. Axis deer persist in only two places. Wild dogs, including dingo, may possibly be the most important natural enemies of deer. Cattle ticks may have a detrimental effect on them in Queensland. The deer herds are not large and do little damage to timber, much of which is unpalatable to these animals.

Accepted for publication October 3, 1956.

A TECHNIQUE FOR SAMPLING MOURNING DOVE PRODUCTION[1]

J. F. Jumber, H. O. Hartley, E. L. Kozicky and A. M. Johnson[2]

Iowa Cooperative Wildlife Research Unit, Iowa State College, Ames

With an increased interest within the state of Iowa on the status of the mourning dove, *Zenaidura macroura* (Linn.), it was deemed advisable to obtain some comparative production figures for Lewis, Iowa, and some surrounding farm areas, where McClure (1943) had worked from 1938 through 1940.

One of the obstacles to be surmounted was the increase in the number of trees within the town of Lewis. In 1938, a survey showed 1,658 trees over 2 inches in diameter on the 160 acres that comprised Lewis, Iowa; whereas, in 1955, there were 3,363 trees. Therefore, it was evident that a complete survey of all trees by one man, the method used by McClure, would not be feasible along with other assignments on mourning dove ecology. Some type of sampling plan was needed.

Field Methods

With McClure's data on 2,886 nests for 1938-1940 revealing that more than 98 per cent of the nests were found in trees, the problem became one of sampling the 3,363 trees for the presence of dove nests. Since no recent information was available on the distribution of dove nests within the town of Lewis, it was decided to stratify the town into 14 strata with each stratum containing about the same number of trees. Further, each stratum was divided into six blocks with each block containing about the same number (40) of trees. The general shape of both blocks and strata was that of a square, depending on the distribution of trees.

Another problem revolved around the difference in tree size; diameter at breast height ranged from 2 to over 40 inches. Some of the smaller trees, depending on species, were easily examined from the ground, whereas others were thought to necessitate climbing for accurate nest counts. A ground count of mourning dove nests was made for all the trees comprising the sampling unit, 40 trees. In addition, a record was made of any tree within the sampling unit when there was any doubt of the accuracy of the ground counts. Then, a random sample of two trees was drawn from the group with doubtful ground counts, and these two trees were climbed. Hence a sample check was made on all trees with doubtful ground counts. No mourning dove nests were found on the ground in Lewis, Iowa, in 1955.

The sampling rate was two blocks a day, and each block necessitated two to three hour's work. With 14 strata in the town, a sample survey of Lewis was made twice every month. The order in which the six blocks in each strata were visited was on a restricted random basis after the first semimonthly period. This order was repeated after the first cycle, May 1 to August 1.

In order to check on the establishment of new nests within any semimonthly period, one set of blocks was retained and a new set was added, one in each stratum. The order in which each of the 14 strata was visited during the semimonthly period was on a restricted random basis.

All observed dove nests were checked with the aid of an offset mirror on a series of 6-foot sections of aluminum pipe. With this instrument it was possible to check nests as high as 40 feet above the ground. Also, it was a simple procedure to obtain the height of the nest above the ground and the distance from the trunk of a tree. A history of all nests was maintained by visiting active nests at least once every three days. Nests that were not successful in producing juvenile doves were deleted from computations on

---

[1]Journal Paper No. J-2961 of the Iowa Agricultural Experiment Station, Ames, Iowa. Proj. No. 1275. Fish and Wildlife Service (U. S. Department of Interior), Iowa State College, Iowa State Conservation Commission, and the Wildlife Management Institute cooperating.

[2]Graduate Assistant, Department of Zoology and Entomology; Professor, Department of Statistics; Leader, Iowa Cooperative Wildlife Research Unit (present address: Department of Conservation, Olin Mathieson Chemical Corporation, East Alton, Illinois); and Graduate Assistant, Department of Zoology and Entomology, respectively, Iowa State College, Ames, Iowa.

mourning dove production; however, their history was used in computing other biological data, such as causes and the amount of nest and nestling destruction, number of eggs, infertility, etc.

The sampling scheme was inaugurated on May 1 and continued to October 1, 1955. No active nests were found between September 15 and October 1. Between April 1 and May 1, 1955, all of the trees in Lewis were checked, but with the advent of leaf foliage, the task became too time consuming for one man.

Although the scheme of checking two trees with doubtful ground counts for mourning dove nests was continued through the sampling period, only once was an additional nest found by climbing. Consequently, the accuracy of the ground counts was beyond expectations and permitted the development of a simpler estimator of dove production and associated variance. However, with different observers and/or species of trees, considerable variation might be found between ground counts of dove nests and counts obtained by climbing the trees.

TABLE 1. — SAMPLING OF MOURNING DOVE PRODUCTION, LEWIS, IOWA, 1955

Semimonthly Period	Blocks	Observed Production[1]	Previous Observed Production[2]	Production
Prior to May 1	All	—	—	24
May 1-15	6	9	2	7
	4	14	4	10
May 16-31	4	17	11	6
	3	11	—	—
June 1-15	3	36	11	25
	5	9	—	—
June 16-30	5	18	4	14
	1	20	—	—
July 1-15	1	12	6	6
	2	11	—	—
July 16-31	2	16	7	9
	6	14	—	—
August 1-15	6	16	6	10
	4	22	—	—
August 16-31	4	14	8	6
	3	2	—	—
September 1-15	3	4	2	2
	5	15	—	—

[1] Observed Production=young produced from eggs in nests started during the period.

[2] Previous Observed Production=young produced from eggs in nests observed during the previous semimonthly period.

RESULTS AND ANALYSIS

The production of mourning doves is estimated by the number of juvenile doves produced from nests observed during the semimonthly sampling periods, regardless of the date that the doves left the nest (Table 1). The normal term of egg laying, incubation, and rearing of young is about 30 days (McClure, 1943).

Prior to May 1 a complete count of dove nests for Lewis was available. Therefore, during the first two weeks of sampling (May 1-15), the number of active nests in blocks 6 and 4 (Table 1) for all 14 strata that started prior to May 1 was known. After the first two weeks, that is, from May 15th onwards, the information for the two blocks differed. One of the two blocks in each stratum, blocks 4 for the period May 15 through May 30, was retained from the previous period and it was possible to record for each of these blocks 4: (1) young produced from eggs in nests started before the beginning of the period, called "Previous Observed Production" in Table 1 (11 young for all blocks 4 combined); (2) young produced from eggs in nests started before the end of the period, called "Observed Production" in Table 1 (17 young for blocks 4); and (3) young produced from eggs in nests started during the period called "Production" in Table 1 (6 young for blocks 4). This is the difference between items (2) and (1). Inasmuch as no information was available on nests started during the previous semimonthly period, May 1 through May 15, for blocks 3, only item (2) "Observed Production" was available for these blocks. If we now assume that the ratio of "Production," item (3), to "Observed Production," item (2), is approximately the same for the two sets of blocks, then an estimate of the "Production" in blocks 3 is given by the ratio estimator:

$$\left(\frac{\text{Production in blocks 4}}{\text{Observed Production in block 4}}\right) \cdot \text{Observed Production in blocks 3}$$

Therefore, substituting from Table 1 (May 16-31):

$$\frac{6}{17} \cdot 11 = 3.9 \text{ young}$$

The mathematical formulation for this ratio estimator is as follows:

y'_s = Actual production from eggs in nests started during the s^{th} semimonthly

period in blocks retained from the $(s-1)^{st}$ semimonthly period

x'_S = Total "observed production" from all eggs in the above blocks during the s^{th} semimonthly period

x''_S = Total "observed production" from all eggs in the blocks newly introduced during the s^{th} semimonthly period.

Then, the ratio estimate for the total production during the s^{th} period is given by

$$3\left[y'_S+\left(\frac{y'_S}{x'_S}\right)x''_S\right] = 3\left[6+\frac{6}{17}\cdot 11\right] = 30 \quad \ldots (1)$$

where the factor 3 allows for the fact that the total area is 3 times as large as the sets of blocks sampled in the 14 strata during a semimonthly period.

The ratio estimator (1) for any semimonthly period after May 15 can be written as follows:

$$\hat{y}_S = 3\,\frac{y'_S}{x'_S}\,(x'_S+x''_S) \quad \ldots (2)$$

The estimator for production for the last eight semimonthly periods after May 15 is therefore given by:

$$\hat{y}_{(S=2,\ldots,9)} = 3\sum_{S=2}^{9}\frac{y'_S}{x'_S}\,(x'_S+x''_S) = \sum_{S=2}^{9}\hat{y}_S \quad \ldots (3)$$

The above estimate is technically known as a ratio estimator in double sampling. The sampling scheme consists of two samples of blocks; that is, the first sample, two blocks from each of the 14 strata, for which the x values are recorded and a second sample (subsample of the first), one block from each of the 14 strata, for which the y value is also recorded.

To this estimate of production (3) will have to be added the estimate of the production prior to the end of the first period (Table 1), i.e. prior to May 15, which we may designate as $\hat{y}_1$:

$$\hat{y}_1 = 3(y_1+y'_1)+24 = 3(7+10)+24 = 75 \quad \ldots (4)$$

Where $3(y_1 + y'_1)$ equals the estimate of mourning dove production between May 1-15 in blocks 6 and 4, respectively, and 24 is the complete enumeration of all young produced from nests in the town of Lewis prior to May 1 (Table 1).

Therefore, the estimate of mourning dove production for Lewis, Iowa, in 1955 may be written:

$$\hat{y} = \hat{y}_1+\hat{y}_{(S=2,\ldots,9)}$$

Substituting from Table 2:

$$\hat{y} = 75+420 = 495$$

In order to estimate the variance of such an estimator, we find that only one y value is available for each of the 14 strata. Therefore, it is necessary to follow the customary device of "collapsing" neighboring strata into 7 strata pairs ($L = 7$) containing 12 blocks each ($N = 12$). Now within each stratum we find a "first sample" of $n' = 4$ blocks was drawn for which x values are recorded, and a second sample (subsample) of $n = 2$ blocks selected from these four blocks for which y values have been recorded as well.

It can now be shown that the estimator $\hat{y}_S$ has the following approximate variance formula:

$$V(\hat{y}_S) = N^2L\left\{\frac{1}{n}\left(1-\frac{n}{n'}\right)S^2_{y-R_Sx}+\frac{1}{n'}\left(1-\frac{n'}{N}\right)S^2_y\right\} \quad \ldots (5)$$

where

S^2_y = the average within stratum variance of the y

$S^2_{y-R_Sx}$ = the average within stratum variance of the $y - R_Sx$ with

TABLE 2. — ESTIMATED PRODUCTION OF MOURNING DOVES, LEWIS, IOWA, 1955

Date	Blocks	Estimated Total Production	Standard Error of Estimate $\sqrt{v}$
Prior to May 1	All	24	
May 1-15	6-4	51	14.0
May 16-31	4-3	30	18.0
June 1-15	3-5	94	36.7
June 16-30	5-1	89	21.5
July 1-15	1-2	35	15.9
July 16-31	2-6	51	19.6
August 1-15	6-4	71	15.0
August 16-31	4-3	21	17.8
September 1-15	3-5	29	11.0
Estimated total production		495	
Standard error of estimated total production			60

R_S defined as the ratio of the populations means; i.e., $R_S = \bar{y}_S / \bar{x}_S$ . . . (6)

This formula agrees with that given by Cochran (1953, p. 282) for the special case of one stratum ($L = 1$) of infinitely large size ($N \to \infty$).

In order to estimate the above variance from the data, let us denote by

$\Delta y'_{si}$ = Difference between the two actual productions in the two blocks in the i^{th} stratum pair retained from the $(s-1)^{st}$ period, where i is the strata pair index.

$\Delta x'_{si}$ = Difference between the two corresponding values of the total production in the same two blocks.

$r_s = y'_s / x'_s$

Using these quantities in conjunction with (5) to obtain an estimate $v(\hat{y}_S)$ of $V(\hat{y}_S)$ or remember that for collapsed strata the variances S_y^2 and $S_y^2 - R_S x$ may be respectively estimated by $\frac{1}{2}(\Delta y'_{si})^2$ and $\frac{1}{2}(\Delta y'_{si} - r_s x'_{si})^2$ so that with $n = 2$, $n' = 4$ and $N = 12$ we obtain here

$$v(\hat{y}_S) = \sum_{i=1}^{7} 144 \left\{ \frac{1}{8}(\Delta y'_S - r_S x'_S)^2 + \frac{1}{12}(\Delta y'_S)^2 \right\}$$

This gives an estimate of the variance of y_S the estimated production during the s^{th} period (for $s = 2, 3, \ldots, 9$). During the first period, y values were observed for both blocks in each stratum and the variance estimation followed standard procedures here as no double sampling occurred; that is,

$$v(\hat{y}_1) = 6 \sum_{c=1}^{14} (\Delta y)^2$$

where Δy denotes the difference between the two values in each of the 14 strata.

The standard errors $\sqrt{v(\hat{y}_S)}$ of the estimates in the individual periods are given in Table 2. Now an estimate of the variance of production during all periods is $v(\hat{y}) = \sum_{S=1}^{9} v(\hat{y}_S)$; which is the sum of the variances of the individual estimates of semimonthly periods. In doing this we have neglected certain correlations in dove production between consecutive periods, but these correlations were estimated to be negligible.

McClure (1943) indicated that production of doves for Lewis, Iowa, 1938-40, averaged 1,108 juvenile doves; consequently, production in 1955, 488 juvenile doves, was only 44 per cent of the 1938-40 level. This drop in production for the town of Lewis may or may not be indicative of southwest Iowa. Mourning doves do shift their breeding populations as indicated by McClure for Lewis in 1938-40. Also, there may be more suitable nesting habitat at the present time throughout southwest Iowa than there was in 1938-40.

SUMMARY

A technique for estimating mourning dove production by making counts of doves fledged from nests located in sample blocks of trees is presented for Lewis, Iowa, for 1955. The semimonthly and annual estimates of dove production and the standard errors of the estimates are given. A comparison of annual dove production is made between the periods 1938-40 and 1955.

LITERATURE CITED

COCHRAN, W. G. 1953. Sampling techniques. John Wiley & Sons, New York. 330 pp.

MCCLURE, H. E. 1943. Ecology and management of the mourning dove in Cass County, Iowa. Bull. 310, Agric. Exp. Sta., Iowa St. Coll., Ames, Iowa.

Received for publication June 4, 1956.

ANIMAL CYCLES AND FOOD

J. Burton Lauckhart

Washington State Game Department, Seattle 9, Washington

The subject of animal-population cycles has been quite thoroughly reviewed in recent literature. Some of the old ideas regarding the cause of such cycles have been reappraised and several new theories have been advanced. Palmgren (1949) and Cole (1951) have proposed that the so-called cycles are merely random fluctuations in animal numbers. Lack (1954b) has concluded that predators may be responsible for the regular cyclic decline in some animal populations, and Siivonen and Koskimies (1955) have presented evidence to show that a lunar cycle may be the immediate cause for these animal cycles. It is not the intention of this paper to disprove any of these theories, but rather to present evidence to show that these cycles may be merely the result of variations in quantity and the nutritive quality of available food.

Braestrup (1940) suggested that a decline in the quality of food as a result of a regular climatic change may cause hare cycles, but subsequent study did not bear out the climatic cycles. He also expressed the belief that nutritional problems may result from overutilization of key food species long before any general overutilization of the food supply is apparent. Grange (1949) proposed that cycles were the result of the interreaction between herbivorous mammals and their food supply. Such a simple cycle, like the waves in the ocean, assumes that the animals' populations build up until they consume all of the food, then die off and rebuild again after the food supply has recovered. Recent studies of lemming populations at Point Barrow, reported by Thompson (1955), suggest a cycle almost that simple. He reports that almost all vegetation was consumed at the peak of the three to four-year cycle. Although Thompson concluded that the cycle was due to a combination of predation and food and cover depletion, it is quite apparent that some cycle would have resulted even if the predators were absent, as most of those lemmings taken by predators were already doomed to starvation. An indication that rabbits may also respond to such a simple starvation cycle is found in reports that they sometimes severely damage their winter food plants during peak years (Bailey, 1946; Grange, 1949; and Cowan, 1950). However, such examples of direct starvation limiting herbivore populations are relatively uncommon in nature, since (in my opinion) malnutrition, not starvation, usually sets the population limits. Most animals resort to so-called "stuffing foods" (Leopold, 1933) rather than succumb to direct starvation. Actually, the rabbits mentioned above which were damaging their ranges, probably were consuming foods that were well below their minimum nutritional requirements.

Most living things have a reproductive capacity that keeps their population at environmental capacity, and the most important single component of that environment is food. This is borne out by Lack (1954a), who concludes that many bird species are "limited in numbers by their food supply." Starker Leopold (1955) gives further support to this conclusion when he states that food is the "all-important" regulator of deer numbers.

Herbivores consume first their sustaining food plants; when these are gone, they turn to marginal food plants, and if they in turn are all used, they must resort to submarginal species that are below their minimum nutritional requirements. However, the difference between the marginal and submarginal foods may be so minute that it cannot be detected by any known method of analysis. During the winter, or bottleneck period, most northern herbivorous populations are in my opinion forced to utilize foods that are nutritionally close to the minimum necessary to sustain life. The pressure of reproduction tends to keep the population at this malnutritional threshold. The animals that are forced below this threshold do not immediately die, but, generally weakened, are less able to protect themselves. They are more susceptible to the attacks of parasites and disease, and they show a lower rate of reproductive survival (Allen, 1954). These

are all symptoms that are commonly found in a cyclic population in its declining phase. For example, Green's work (1939) on "shock disease" of rabbits suggests a nutritional deficiency as the primary cause. MacLulich (1937) showed that several diseases may be involved in the decline of some cyclic species. Low reproduction, or low survival of young, has been found in most studies of the decline of cyclic animals (Bump, *et al.*, 1947; Edminster, 1947; Siivonen, 1952; Lack, 1954a). These correlations are circumstantial evidence that cyclic decline is nutritional, probably associated with either a decline in the quantity or quality of the food supply.

Koskimies (1955) suggests that cyclic losses of northern herbivores are biologically necessary to protect the slow-growing northern vegetation from overutilization. It seems that the cycles must have some survival value, or the animals would have developed adaptations to overcome them. Apparently the animals and their food plants evolved together and those that overutilized and destroyed their food supply also destroyed themselves (Allee, *et al.*, 1949; Koskimies, 1955). For example, if a grouse were evolved that could thrive on any or all of the twigs and buds of coniferous trees, there would be little to halt its increase until all conifers were killed, because there is no way in which a tree could escape from a horde of hungry birds. However, if there were several species of coniferous food plants present, each of a different nutritional value, the birds would undoubtedly overutilize and possibly kill the ones of high food value, but the trees of marginal quality could probably survive. They would be protected if only a part of the foliage of an individual tree were nutritionally adequate to serve as grouse food, or if only a few individual members of a plant species were vigorous and rich enough to sustain birds. Marginal plants may also protect themselves by some regular cyclic decline in their nutritional value, or utilization alone may so weaken them that their remaining foliage drops below the nutritional threshold. These are all possible methods by which marginal plants may retreat below the nutritional minimum required by animals. It would seem that all plants must develop some method of escape from total utilization by herbivorous animals with the result that many have evolved near to this malnutritional threshold.

There is some evidence to bear out this theory that tree buds are very low nutritionally. Grange (1948) reports that ruffed grouse (*Bonasa umbellus*) were found budding at sunset and again at sunrise, but in extremely cold weather they are already in the trees in search of buds when the stars are still shining before dawn, and with such temperatures they will again be budding after sunset. He also reports that on such occasions they may fill their crops almost to the "bursting point." This extreme effort apparently is necessary to nourish the bird with this low-value food. Hamerstrom, Hopkins and Rinzel (1941) experimented with the feeding of captive pinnated grouse (*Tympanuchus cupido*) but were unsuccessful in attempts to winter them on buds alone. Siivonen (1954), Koskimies (1955) and Grange (1948) all report that grouse show a decided preference for certain trees and sometimes feed on an individual tree for some time. This suggests that there is a difference in the food value of individual trees. Undoubtedly the fertility of the soil, the site, exposure to the sun, and the age of the tree all have a part in determining the food value of the buds. Apparently the birds can distinguish which buds and twigs are nutritionally adequate. If grouse and other northern herbivores are teetering on this brink of malnutrition, any regular, though minute, change in the nutritional quality of their food could cause cycles. With this in mind, ecologists have attempted to tie cycles to all types of external forces, but with questionable success.

There is still one seemingly obvious cycle of plants that apparently never has been considered as a cause for animal cycles. This is the *reproductive cycle.* In tropical and temperate climates where there apparently are no animal cycles, the plants largely produce seed every year, but in the northern regions a greater spacing of seed crops is general. As we proceed northward we find the seed years becoming progressively more pronounced and animal cycles also increasing in magnitude.

Evidently, northern plants are unable to produce enough food in a single, short, growing season to yield a yearly seed crop. Thus they must manufacture and store

nutrients for several years before the seed can be produced. According to the *Woody-plant Seed Manual* of the United States Forest Service (1948), "Many forest trees and shrubs produce good seed crops at regular intervals. Some bear good crops every year, some every second or third year, and some at longer intervals—up to 10 or more years." The manual further states that an explanation for seed cycles widely accepted by foresters is based on Hartig's work with European beech—that food reserves stored in the stems are exhausted by production of a heavy seed crop, and a number of years is required to replenish them.

Frederick Baker in his book on *Principles of Silviculture* (1950) states that "Close observation often reveals the presence of fairly regular (seed) cycles with years of excellent production alternating with off years." He states further: "Periodicity of European Beech is marked. It appears that starch is accumulated in the parenchyma of the sapwood for a period of about eight years. It is then almost completely expressed in a seed crop, following which accumulation is again resumed."

Since so many cyclic birds and mammals in the lower layer of the animal pyramid feed on twigs and buds, it seems quite logical that they may be affected by these food changes. It is quite possible that a heavy seed crop may so sap the nutrients from the stems and buds that the entire food supply may drop below the nutritional level necessary for successful reproduction, and this deficiency might continue one, two, or even more years until the nutrients are replenished. Some typical seed-year frequencies as given by the *Woody-plant Seed Manual* (*op. cit.*) are as follows: larch (*Larix* sp.)—5 to 6 years, apple (*Malus* sp.)—2 years, spruce (*Picea* sp.)—2 to 8 years, varying with the species, pine (*Pinus* sp.)—3 to 5 years, aspen (*Populus tremuloides*)—4 to 5 years, white cedar (*Thuja occidentalis*)—5 years, and hemlock (*Tsuga* sp.)—2 to 5 years. The most common intervals appear to be three-year and four-year cycles that fit very well with Siivonen's (1952) findings with regard to the short-term, or 3-1/3-year, cycle of tetraonids. Where there is only one primary winter-food plant, the populations of animals that feed upon it should fluctuate directly with its seed cycle. Their peak number should occur in the summer and fall that the seed is formed, and their decline should start in the winter following this seed year when the twigs have been sapped of their stored food. However, if there are two important food plants available that are out of step in their seed cycles, the animals may concentrate on one when the other is in its low nutritional phase, but undoubtedly they will at times get the seed cycles together and thus produce a much longer animal cycle. Thus, it may be possible to have a ten-year cycle produced by the interreaction of two short-term cycles. Where there are many varieties of winter-food plants available in near equal quantities, there will probably be no animal cycle.

Populations of seed-eating animals should peak one year later than those that feed on foliage and buds. The winter following the seed crop is the most abundant food period for squirrels and is also the most critical period for grouse and other twig and bud eaters, as the seed crop has already drained all of the nutrients from the plant. For example, Lampio (1952) reports that Finnish squirrels were in peak abundance in 1946, while Siivonen (1952) states that Finnish grouse were present in greatest numbers in 1944 and 1945. Siivonen (1954) has also shown that small rodents have consistently peaked one year later than grouse. In a forested region such as Finland, small rodents are largely of seed-eating species.

Climatic factors can influence the normal seeding cycle of a plant. Lampio (1952) reports that a seed crop in spruce is initiated by a warm, dry period in late June and July. This starts the blooming buds, but the seed will not be available until the end of the next summer. Baker (1950) states that cold, wet, growing seasons lengthen the seed cycle for forest trees, particularly for species near their northern limits. He also indicates that "The destruction of a potentially heavy crop of flowers prevents the expenditure of stored nutrients, or otherwise upsets the normal cycle and commonly calls forth a heavy crop the following year." Such a delay increases the reserve of stored nutrients in the plant and should result in a better crop of birds and mammals that feed upon it. On the other hand, a series of small or partial seed crops could prevent the build-up of food in a plant and thus may retard the

recovery of the animals that use it for food.

It is the opinion of the author that this seed-cycle theory will explain the fluctuations in abundance of some of the so-called cyclic birds and mammals. The production of seed probably is not the causative force behind all cycles, as the lemming cycles described earlier would indicate, but it is a plausible explanation for some grouse fluctuations that have been very baffling. The seeming abundance of winter grouse food has in the past largely precluded the consideration of food as a limiting influence on these birds. Food appears to be the most important environmental component affecting the abundance of animals and nutritional problems probably are in some way involved in most animal cycles.

SUMMARY

A simple cycle resulting from population build-up, to the point of complete food depletion, followed by animal starvation and subsequent recovery of food plants, appears to be responsible for some variations in rodent abundance. In this paper, it is argued, however, that malnutrition resulting from utilization of foods that are nutritionally submarginal is much more common than actual starvation. Disease, lowered reproduction, and reduced survival of young, all of which are symptoms of cyclic decline, are also associated with malnutrition. There is some evidence that buds and twigs of northern trees, the food supply of northern herbivores, are very low in nutritional value so that a slight change could bring on malnutrition.

An obvious cycle of northern plants that could cause a nutritional change is the reproductive or seed cycle. Both the animal cycles and the seed-year cycles become more pronounced as we go north. Botanists assume that northern plants must manufacture and store food for several years to produce a single seed crop, and when the seed is produced, this crop utilizes all of the stored nutrients from the twigs and stems. It seems logical that herbivores feeding on these plants would be influenced by these changes in stored nutrients. The most common seed cycle is about 3 1/2 years which is very similar to the short-term cycle described for some Finnish animals. However, interreacting seed cycles could cause much longer animal cycles. Unfavorable weather can prevent the start of a seed crop and thus lengthen any cycle.

LITERATURE CITED

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK AND K. P. SCHMIDT. 1949. Principles of animal ecology. Saunders, Philadelphia and London. xii + 837pp.

ALLEN, DURWARD L. 1954. Our wildlife legacy. Funk and Wagnalls, N.Y. 422pp.

BAILEY, ROBERT A. 1946. Reading rabbit population cycles from pines. Wis. Cons. Bull., 11 (7):14-17.

BAKER, FREDERICK S. 1950. Principles of silviculture. McGraw-Hill, New York. 414pp.

BRAESTRUP, F. W. 1940. The periodic die-off in certain herbivorous mammals and birds. Science, N.S. 92:354-355.

BUMP, G., R. W. DARROW, F. C. EDMINSTER AND W. F. CRISSEY. 1947. The ruffed grouse. New York Cons. Dept., Albany, N.Y. 915pp.

COLE, L. C. 1951. Population cycles and random oscillations. J. Wildl. Mgmt., 15:233-252.

COWAN, I. McT. 1950. (in discussion) Trans. N. Amer. Wildl. Conf., 15:382.

EDMINSTER, FRANK C. 1947. The ruffed grouse. Macmillan Co., N.Y. 385pp.

GRANGE, WALLACE B. 1948. Wisconsin grouse problems. Wisconsin Cons. Dept., Madison, Wis., 318pp.

———. 1949. The way to game abundance. Scribner's, N.Y. 365pp.

GREEN, R. G., C. L. LARSON, AND J. F. BELL. 1939. Shock disease as the cause of the periodic decimation of the snowshoe hare. Amer. J. Hyg., 30(3):83-102.

HAMERSTROM, F. N., J. F. HOPKINS AND A. J. RINZEL. 1941. An experimental study of browse as a winter diet for prairie chicken. Wilson Bull., 53(3):185-195.

KOSKIMIES, JUKKA. 1955. Ultimate causes of cyclic fluctuations in numbers in animal populations. Finnish Game Foundation, Papers on Game Research, 15:1-29.

LACK, DAVID. 1954a. The natural regulation of animal numbers. Oxford Univ. Press, Oxford. 343pp.

———. 1954b. Cyclic mortality. J. Wildl. Mgmt., 18:25-37.

LAMPIO, TEPPO. 1952. Squirrel hunting based on the ecology of the species. Finnish Game Foundation, Papers on Game Research, 8:44-49.

LEOPOLD, ALDO. 1933. Game management. Scribner's, N.Y. 481pp.

LEOPOLD, A. STARKER. 1955. Too many deer. Sci. Amer., 193(5):101-108.

MACLULICH, D. A. 1937. Fluctuations in the num-

bers of the varying hare (*Lepus americanus*). Univ. of Toronto Studies Biol. Ser., 43:1-136.

PALMGREN, P. 1949. Some remarks on the short-term fluctuations in the numbers of northern birds and mammals. Oikos, 1:114-121.

SIIVONEN, LAURI. 1952. On the reflection of the short-term fluctuations in numbers in the reproduction of tetraonids. Finnish Game Foundation, Papers on Game Research, 9:1-43.

———. 1954. On the short-term fluctuations in numbers of tetraonids. Finnish Game Foundation, Papers on Game Research, 13:1-10.

——— AND J. KOSKIMIES. 1955. Population fluctuations and the lunar cycle. Finnish Game Foundation, Papers on Game Research, 14:1-22.

THOMPSON, DANIEL Q. 1955. The role of food and cover in population fluctuations of the brown lemming at Point Barrow, Alaska. Trans. N. Amer. Wildl. Conf., 20:166-176.

U.S. FOREST SERVICE. 1948. Woody-plant seed manual. U.S. Dept. Agric., Misc. Pub., No. 654. 416pp.

Received for publication May 21, 1956.

OBITUARY

NATHAN WARREN FELLOWS, JR.
1915-1956

Nathan W. Fellows, Jr., was killed in an airplane accident August 27, 1956, while conducting his official duties as regional biologist for the Maine Department of Inland Fisheries and Game.

"Nat" or "Nate," as his friends called him, was born August 16, 1915, at Beverly, Massachusetts. An honor student and member of the Phi Kappa Phi honorary society, he received a B.S. degree in wildlife conservation (minor in forestry) from the University of Maine in 1938. He was employed as a field technician by the Maine Department of Inland Fisheries and Game from May 1939 to August 1939, and after working as a conservation warden in Rhode Island from August 1939 to February 1941, he returned to Maine to serve as a field technician and later as a project leader.

This work was interrupted on February 17, 1943, when Nat began active duty in the Navy as an ensign. He was subsequently elevated in rank to Lt. (j.g.) and saw active combat in the Pacific theater while in command of a ship, PC 1229. He was awarded the Atlantic and Pacific Campaign Ribbons, National Defense Ribbon, Naval Reserve Medal, World War II Victory Medal, and the Philippine Campaign and Occupation Ribbon. He maintained his interest in the Navy after being released from active duty in April 1946 by joining the Naval Reserve. His efforts were rewarded by his promotion to Lt. Commander on March 1, 1952.

He returned from active duty in the Navy to his position as project leader for the Maine Department of Inland Fisheries and Game and was promoted to the position of Biologist II in February 1949. He was again recalled to active duty from October 1950 to September 1952, serving in Japan and Greenland. From 1952 until his death he again worked for the Department.

Professionally, Nat became an active member of The Wildlife Society in 1944. One of his primary interests in game-management work was in the field of waterfowl investigations and development work. At one site in particular (the Abagadassett River at Merrymeeting Bay) where he had conducted several annual waterfowl bag checks, Nat was sought out by many hunters for reliable information on the identification of their ducks, the hunter success in the area, and for conversations in general. He was an excellent observer both on the ground and in the air. In 1952, he published "Waterfowl Food Plantings Survival," a bulletin of the Department dealing with his studies of the survival of waterfowl foods planted throughout the state in 1939 and 1940. He was very well liked and was making big strides in game-management work as a regional biologist in the western part of the state. His interests also included a survey of the importance of game and fur bearers to the economy of the state about which he wrote two reports.

Through his varied career, Nat made many friends and he will be greatly missed and long remembered for his natural ability in game-management work, his keen sense of humor, and his friendly nature. Nat's family, to whom he was greatly devoted, consists of his wife Ginny, an 8-year-old daughter Judy, and a 5-year-old son Jeff.

—KENNETH W. HODGDON.

BRIEFER ARTICLES

FOOD OF WOOD DUCKS IN MAINE[1]

Malcolm W. Coulter

Maine Cooperative Wildlife Research Unit

Little specific information concerning the food eaten by wood ducks (*Aix sponsa*) is available. Populations of these birds have been relatively low. For many years they were completely protected, and even today special regulations restrict the shooting of wood ducks. This situation has made it difficult to study their food habits in detail.

During the period from 1938 to 1953, stomachs (gizzard and gullet) from wood ducks were submitted to the Maine Cooperative Wildlife Research Unit by state game wardens, hunters, and field personnel of the Department of Inland Fisheries and Game. This report summarizes the results of the analysis of these stomachs.

Materials and Methods

Seventy-six stomachs taken during the summer or fall were available for examination, of which 11 contained insufficient food for tabulation. The remaining 65 specimens were taken from 20 freshwater streams or marshes scattered throughout the state.

Stomach contents were washed, separated, and measured. Tabulation of food items was by the "percentage-by-bulk" method as practiced by the U.S. Fish and Wildlife Service. In common with other systems for presenting food-habits data, this method has certain disadvantages. The most common error occurs when a few individuals contain large quantities of a single food item. Such instances are qualified in the text.

Results

Table 1 presents the major foods found in 54 stomachs taken during September or October. It is apparent that animal foods were eaten in small quantities and by less than a third of the ducks.

Table 1. — Fall Foods of Wood Ducks in Maine (54 Stomachs)

	Percentage of Total Food	Number Specimens
Vegetable food—95.0 per cent		
Wild rice (*Zizania aquatica*)	15.0	11
Pondweeds (*Potamogeton* spp.)	12.5	26
Bur-reeds (*Sparganium* spp.)	12.0	29
Water bulrush (*Scirpus subterminalis*)	11.0	11
Oaks (*Quercus* spp.)	9.0	6
Pickerel weed (*Pontederia cordata*)	5.0	9
Dogwood (*Cornus* spp.)	5.0	8
Arrowhead (*Sagittaria* spp.)	4.5	7
Other plant food (19 species)*	14.5	
Unknown	6.5	17
Animal food—5.0 per cent		
Insecta	5.0	16
Gastropoda	trace	2

* Water-plaintain (*Alisma plantago-aquatica*), watershield (*Brasenia schreberi*), sedges (*Carex* spp.), twig-rush (*Cladium mariscoides*), three-way sedge (*Dulichium arundinaceum*), spike-rush (*Eleocharis* spp.), rush (*Juncus* spp.), holly (*Ilex* spp.), rice-cutgrass (*Leersia oryzoides*), white pine (*Pinus strobus*), spruce (*Picea* spp.), wild cherry (*Prunus* spp.), arrowhead (*Sagittaria cuneata*), Torrey's three-square (*Scirpus torreyi*), wool-grass (*Scirpus cyperinus*), bulrush (*Scirpus* spp.), cranberry (*Vaccinium* spp.), mermaid weed (*Proserpinaca palustris*), and wild celery (*Vallisneria americana*).

Among the plant foods, eight genera made up three-quarters of the material. Except for wild rice and the oaks, the major foods are from plants that are common in almost all waterways in Maine.

Data concerning the foods eaten by eight wood ducks from the ages of three or four days to seven weeks are presented in Table 2. The importance of animal food to young birds is apparent. The animal food consisted almost entirely of insects. Twenty-two kinds of insects were identified. Those that occurred most frequently were dragon flies and damsel flies (Odonata); water boatmen, water striders, and leaf bugs (Hemiptera); and leaf beetles and snout beetles (Coleoptera). Nine species of plants were identified. However, seeds of manna-grass (*Glyceria borealis*) and of sedges (*Carex* spp.) were eaten in quantity by four birds. One stomach, taken in late August, contained about 150 unripened wild rice seeds.

[1] Contribution from the Maine Cooperative Wildlife Research Unit, Orono, Maine; Maine Department of Inland Fisheries and Game, University of Maine, Wildlife Management Institute, and the U.S. Fish and Wildlife Service cooperating. Appreciation is expressed to Howard L. Mendall for help in examining stomachs and in preparation of the manuscript; to Jay Gashwiler and Joel Marsh who examined part of the early collections; and to staff members of the Department of Botany and the Department of Zoology, University of Maine, for assistance in identifying some food items.

TABLE 2. — FOOD OF FLIGHTLESS YOUNG WOOD DUCKS (8 STOMACHS)

Approximate Age of Duckling	Percentage of Food by Bulk	
	Insects	Plants (Mostly Seeds)
4 days	100	0
1-2 weeks	57	43 (grasses and sedges)
1-2 weeks	66	34 (unidentified vegetation)
1-2 weeks	46	54 (grasses)
3-4 weeks	3	63 (grasses)
		34 (aquatic plants)
5 weeks	19	81 (grasses)
5 weeks	71	29 (bur-reeds and pondweeds)
7 weeks	4	96 (wild rice)

DISCUSSION

The indicated use of wild rice by adult birds is somewhat misleading. Remains of this species were found in 11 (20 per cent) of the duck stomachs. In 9 of the 11 cases, the large quantities of wild rice consumed made this plant appear to be the leading food for the sample. Actually, wild rice is available for only a short period during early autumn. In a few waterways of Maine it thrives; in most areas it is absent or, when present, the plants grow in sparse, unthrifty stands that fruit irregularly. However, when available, wood ducks appear to feed upon the fruits of this plant almost to the exclusion of other foods.

Four species of pondweeds were identified. Floating-leaf pondweed (*Potamogeton natans*) made up over half the material from this group of plants. It is extremely common throughout Maine, and it regularly produces large quantities of fruit. During late summer and autumn the seeds constitute one of the foods most readily accessible to surface-feeding ducks.

Bur-reeds were also important in the sample examined. Seeds and seed husks made up most of the material found. Specific identification of bur-reed seeds from duck gizzards is often impossible. However, it was evident that four common species, *Sparganium chlorocarpum, S. fluctuans, S. angustifolium,* and *S. minimum,* were taken. Bur-reeds, as a group, were considered important as fall and spring food of the black duck (*Anas rubripes*) in inland fresh waters in Maine by Mendall (1949. Food habits in relation to black duck management in Maine. J. Wildl. Mgmt., 13:64-101). They also made up a significant proportion of the spring foods of black ducks and wood ducks examined by Coulter (1955. Spring food habits of surface-feeding ducks in Maine. J. Wildl. Mgmt., 19:263-267). The available evidence suggests that bur-reeds deserve careful consideration in any program designed to increase the supply of plant food for ducks, as for example, in newly created impoundments.

Sedges are conspicuously absent from the list of leading foods. In other studies in Maine and elsewhere, plants in the sedge family are important foods for surface-feeding ducks. Except for water bulrush in the present study, sedges were not found in quantity although several kinds of sedges are abundant in the state. Seeds as well as vegetative parts of water bulrush are eaten. Tubers from this plant are an important food during the autumn. Well-developed tubers are not present on the plants during the growing season.

Acorns were taken by only six birds, but as was the case with wild rice, those ducks that fed upon acorns consumed large amounts. Oak trees are not predominant in the northern two-thirds of Maine. Yet field observations have indicated that wherever oak trees occur near water, wood ducks sometimes forsake available aquatic foods to feed avidly upon acorns.

The other leading foods, pickerel weed, dogwood, and arrowhead, are common along almost all waterways. In view of the abundance of pickerel weed from the collection areas, as well as this plant's habit of fruiting abundantly, it is surprising that more seeds from pickerel weed were not taken. A similar lack of use of this plant has been noted in previous studies of foods eaten by ducks in Maine.

The 19 species of plants that made up the remaining 15 per cent of the food each occurred in small amounts and in few specimens. Most of the plants represented are common in or near waterways throughout the state.

The food from three additional stomachs taken from adults killed in August contained mostly plant material. Two birds had fed heavily upon pondweeds; the stomach of the other contained stems and leaves of royal fern (*Osmunda regalis*).

SUMMARY

Examination of the foods eaten by 65 wood ducks taken in Maine revealed that full-grown birds fed heavily upon pondweeds, bur-reeds, water bulrush, and upon wild rice and acorns when the latter two were available. Flightless young consumed large quantities of insects. Some common aquatic plants were seldom utilized as food.

Received for publication September 17, 1956.

THE FOOD OF FUR SEALS IN THE EASTERN BERING SEA

Ford Wilke and Karl W. Kenyon

Branch of Wildlife Research, U.S. Fish and Wildlife Service, Seattle 15, Washington

The development of commercial fisheries in the Aleutian area, particularly the catching of salmon in the open sea with drifting gill nets, has stimulated interest in the food of the Pribilof seal (*Callorhinus ursinus*) in the Bering Sea. Added interest results from the decline in the salmon runs in Bristol Bay. Fisheries investigators believe that at least part of the salmon migrating to rivers entering Bristol Bay pass through areas in the Bering Sea where fur seals feed intensively. No pelagic investigation of the food of fur seals while in the Bering Sea has been made since Alexander's in 1892. This was summarized by Lucas (1899) who wrote that "In Bering Sea during August and September the pollack (*Theragra chalcogramma*) forms the staple article of food, a squid (*Gonatus amoenus*) coming next in importance, while some salmon and a few species of small fish are also eaten." Lucas quotes Alexander in stating that "material which has been found in the stomachs of seals taken in different parts of Bering Sea indicates that only a small percentage is composed of fish which inhabit deep water. It is only reasonable to suppose that when seals are in shallow water they feed on both bottom fish and those near the surface." Lucas footnoted the latter part of this statement, saying: There is, however, no evidence of this except in the rare presence of cottoids. . ." On the basis of stomachs collected from the killing fields, Kenyon (1956) has verified Alexander's statement. Most of the content of these stomachs (94 per cent) was composed of sand fish (*Trichodon trichodon*), which burrow in sand in relatively shallow water. The sturgeon-like sea poacher (*Agonus acipenserinus*), second in importance, is also a bottom dweller.

From 17 June to 20 July 1955, 204 fur seals were collected pelagically in the Bering Sea from Unimak Pass and Unalaska to the Pribilof Islands. Most of the seals were collected by the authors by shooting with buckshot from the deck of a halibut schooner, the *M/S Paragon*. On the rare calm days two men worked from a dory powered with a 10-horsepower outboard. In good weather this was as effective as the larger vessel, and fewer animals were lost when hunting with the dory. Throughout the period, seals were most abundant in or near Unimak Pass. Near the Pass were also Steller sea-lions (*Eumetopias jubata*), numerous humpback whales (*Megaptera novaeangliae*), and vast numbers of shearwaters (*Puffinus* spp.). It is reasonable to presume that the rich food supply attracted all these forms. Pregnant females predominated among the seals collected, comprising 71 per cent of the total. Females without fetuses composed 16 per cent and males 13 per cent of the collection.

Table 1 gives the food contained in the stomachs of 204 seals collected pelagically and of three others in the commercial kill at St. Paul Island where empty stomachs are the normal condition among the thousands we have examined.

Capelin was the predominant food species in Unimak Pass and near the Aleutian Islands. It appears that concentrations of capelin are available for the seals during extensive portions of their northward migration. Scheffer (*in* Taylor, Fujinaga, and Wilke, 1955) found that capelin made up more

TABLE 1. — CONTENTS OF 117 FUR SEAL STOMACHS CONTAINING FOOD, COLLECTED IN THE BERING SEA AND ON ST. PAUL ISLAND[1]

Where Collected	Contents	Percentage of Food by Volume	Frequency of Item
Bering Sea[1]	Salmon (*Oncorhynchus* sp.)	0.5	1
	Capelin (*Mallotus villosus*)	52	45
	Alaska pollack or whiting (*Theragra chalcogramma*)	40	36
	Sand lance (*Ammodytes tobianus personatus*)	trace	1
	Unidentified fish	1	2
	Squid (Decapoda)	7	56
	Miscellaneous mollusks, probably not food		
	Rough thais (*Thais lima*)	trace	1
	Heavy-ribbed venus-heart (*Venericardia crebricostata*)	trace	2
	Dire-whelk (*Searlesia dira*)	trace	2
St. Paul Island[2]	Salmon (*Oncorhynchus* sp.)		1
	Alaska pollack or whiting (*Theragra chalcogramma*)		1
	Sand fish (*Trichodon trichodon*)		2

[1]Bering Sea, 114 stomachs, total stomachs, 204. Total empty stomachs, 90.

[2]Commercial kill, 3 stomachs. Percentage of food by volume not obtained, since stomachs were recovered in slashed and partly drained condition.

than 90 per cent of the food of seals taken in the western part of the Gulf of Alaska from the Kenai Peninsula to Afognak Island in June 1955. The capelin is an arctic species (Clemens and Wilby, 1946) reaching its southern limit along the Olympic Peninsula of Washington.

Squid ranks high in frequency but low in volume, for two reasons. First, squids are more available at night and thus are usually well digested by the time a seal that has fed on squid is taken during daylight hours. Secondly, they are soft bodied and only the beak, eye lenses, and pens resist digestion. The abundance of these hard parts indicates that squids are a staple food, but whole squids or even large quantities of their flesh are only occasionally found.

Except for salmon, which occurred once in the pelagic sample and once in stomachs collected on land, none of the food species found in this sample enter into any commercial fishery in North America. The Alaska pollack or whiting at present is not acceptable as a market species, being rather thin and soft fleshed. A single seal taken in March 1955 had stomach contents composed entirely of Alaska pollack. A squid fishery is carried on in California for a limited market, but no squids are taken in northern waters. From their infrequent appearance in seal stomachs it appears that salmon are rarely available as prey species and the relationship between free-swimming salmon and fur seals is that of co-predators rather than predator and prey. In an artificial situation, such as where salmon are caught in a gill net, fur seals will feed on them readily.

No herring (*Clupea pallasi*) appeared in the stomachs although a population of commercial size is present near Unalaska Island. It is noteworthy that herring populations have currently reached high levels in southeastern Alaska and British Columbia despite predation by fur seals and numerous other forms. The greatest herring catch in British Columbia history took place in 1955-56, and the great abundance of herring in southeastern Alaska waters is not reflected in the restricted catch.

SUMMARY

In the stomachs of 117 fur seals collected between Unimak Pass and the Pribilof Islands in the Bering Sea, capelin was the dominant food near the Aleutian Islands (52 per cent of total food by volume) and was replaced offshore by squid and Alaska pollack which there made up 47 per cent of total food by volume. Salmon (which pass through this area in migration) and sand lance each appeared once. Salmon, Alaska pollack, and sand fish made up the contents of 3 stomachs from St. Paul Island.

LITERATURE CITED

CLEMENS, W. A. AND G. V. WILBY. 1946. Fishes of the Pacific Coast of Canada. Fisheries Res. Bd. Canad., Bull. 68:97.

KENYON, K. W. 1956. Food of fur seals taken on St. Paul Island, Alaska, 1954. J. Wildl. Mgmt., 20:214-215.

LUCAS, F. A. 1899. The food of the northern fur seals. *In* The fur seals and fur-seal islands of the North Pacific Ocean, by D. S. Jordan, *et al.* U.S. Treas. Dept. Doc. 2017, part 3, pp.59-68.

TAYLOR, F. H. C., M. FUJINAGA, AND F. WILKE. 1955. Distribution and food habits of the fur seals of the North Pacific Ocean. Report of cooperative investigations by the governments of Canada, Japan, and the United States of America, February-July, 1952. Govt. Print. Off., Washington, D.C. x + 86pp.

Received for publication October 8, 1956.

DISPHARYNX NASUTA IN HUNGARIAN PARTRIDGE IN ONTARIO

J. F. Bendell and R. D. Lisk

Department of Zoology, University of British Columbia, Vancouver 8, B.C.

In the summer of 1955 the Toronto Anglers' and Hunters' Association financed a study of the Hungarian partridge (*Perdix perdix* L.) in Ontario. Two adult and four birds-of-the-year from the Niagara Peninsula were autopsied. The two adult birds were infected with *Dispharynx nasuta* Rud. Two adult and ten young-of-the-year partridge were collected near Kemptville in eastern Ontario. Two young-of-the-year were infected with *D. nasuta*. These records are the first report of *D. nasuta* in Ontario.

Yeatter (1934) reports *D. nasuta* in Hungarian partridge in Michigan. The present distribution of partridge is continuous from Michigan to and beyond the eastern part of Ontario (Aldrich and Duvall, 1955). This and the first occurrence of *D. nasuta* suggests that some Hungarian partridge in Ontario are descendants of emigrants from Michigan that carried *D. nasuta* into the province with them.

LITERATURE CITED

ALDRICH, J. W. AND A. J. DUVALL. 1955. Distribution of American gallinaceous game birds. U.S. Dept. Int., Fish and Wildl. Serv., Cir. 34. 30pp.

YEATTER, R. E. 1934. The Hungarian partridge in the Great Lakes Region. Univ. Mich. School Forestry and Cons., Bull. 5. 92pp.

Received for publication November 21, 1956.

STRESS RESPONSE AND SURVIVAL TIME IN THREE WILDLIFE SPECIES[1]

Ruth L. Hine and Kenneth G. Flakas

Wisconsin Conservation Department, Madison

The need for studies on the ability of various wildlife species to survive and the factors affecting their survival has become increasingly important in wildlife management research. Such information is not only essential for an understanding of population behavior but also for planning habitat improvement programs designed to meet specific requirements.

One approach toward obtaining physiological information of this type is by subjecting an animal to an applied stress and measuring its resistance and survival time. Kabat, Meyer, Flakas, and Hine (1956) in Wisconsin carried out a series of experiments throughout the year on hen pheasants (*Phasianus colchicus torquatus*) in which they subjected the birds to the artificial stress of caging and starvation and measured the birds' resistance in terms of body-weight loss and body-temperature decline. The design of their studies was based on Selye's (1949) hypothesis that adaptation to a specific stress (such natural stresses as egg laying, molting, etc.) lowers the body's resistance to different stress to which the animal is not adapted. The applied stress, therefore, was used as a means of demonstrating whether there was seasonal variation in adaptation energy, and which of the naturally occurring physiological stresses caused the greatest decrease in resistance. These studies showed that the use of this technique appeared to produce reliable trends in stress resistance and survival time. There was variation in the hen pheasant's ability to survive the applied stress at different times of the year; this variation in stress resistance and survival time, furthermore, was related to the physiological condition of the hen.

The hen pheasant studies opened the door to much more investigation along these lines. During the course of the Wisconsin pheasant experiments in January to March 1951, single tests were run on Hungarian partridge (*Perdix perdix*), chukar partridge (*Alectoris graeca chukar*), and cottontail rabbits (*Sylvilagus floridanus*). The purpose of this report is to present the results of these tests in order to document the data and provide background information for other investigators contemplating similar studies.

Methods

The animals used for these tests came from the following sources in Wisconsin: 8 Hungarian partridge (4 hens and 4 cocks) were trapped in Milwaukee County; 8 chukar partridge (4 hens and 4 cocks) were taken from game-farm stock at Poynette; and the 13 cottontails were trapped in the vicinity of Madison and Poynette.

The standardized stress regime that has been previously described (Kabat, *et al.*, 1956) was used. For the experiments, the animals were placed in wooden cages varying from 69 to 49 inches long, 22 inches wide, and 15 inches high. These were kept in an unheated building. The cages used for both species of partridge were darkened by placing cardboard over one-half to one-third of the screened area in order to quiet the birds. The stress periods varied from 10 to 12 days. During this time no feed was given, although fresh water was supplied daily. On the first day of stress and at one or two intervals during the stress period, body-weight and body-temperature measurements were taken, and cloacal cultures and blood smears were made. Post-mortem examinations were made on all animals that died.

All Hungarian partridge and rabbits died during the tests so that the average survival time represents an average of the actual number of days these animals survived the applied stress. Since no chukars were lost during the 12-day stress period, average survival time is an estimate of the number of days these birds might have lived under continued stress, based on the weight-loss and body-temperature-decline data.

Results and Discussion

The results of these experiments (Table 1) show the amount of weight loss and the survival of these species. The trends indicate the resistance of the animals to an applied stress. Detailed comparisons of stress response and survival between species, however, cannot be made as the data were not collected for this purpose. The animals came from different sources, game farm and wild; and the experiments were run in different months. However, a few general inferences may be drawn from the information at hand.

The data presented in Table 1 suggest that differences do exist between these species in their ability to withstand applied stress. In the case of the two partridge species, these differences may be related to the initial weight of the birds. The chukars were about 200 grams heavier than the Huns at the beginning of the stress period; they lost weight less rapidly and survived longer than did the Huns. In the hen pheasant, a general relationship exists throughout most of the year between the weight of the bird at the start of the stress period and the length of time it survived the stress (Kabat, *et al.*, 1956). The rabbits, however, were almost

[1] A contribution of Pittman-Robertson Research Project 24-R. The writers wish to thank Cyril Kabat and James B. Hale for their advice and assistance.

TABLE 1. — RESPONSE OF CHUKAR PARTRIDGE, HUNGARIAN PARTRIDGE, AND COTTONTAIL RABBITS TO APPLIED STRESS

	Chukar Partridge	Hungarian Partridge	Cottontail Rabbit
Date	March 1951	February 1951	January 1951
No. animals	8	8	13
Av. weight in grams (and per cent loss)			
Initial	560	372	1,161
7th stress day	476 (15%)	269 (27%)	970 (16%)*
12th stress day	399 (29%)	—	—
At death	—	221 (41%)	900 (22%)
Av. body temperature (F.)			
Initial	108.9°	106.9°	100.8°
7th stress day	107.4°	105.3°	98.9°*
12th stress day	105.8°	—	—
Av. survival (days)	ca. 15	10	10

* 8th stress day

three times heavier than the Hungarian partridge, but both species survived the applied stress the same length of time.

On the other hand, these differences in stress resistance and survival may be a manifestation of an actual difference in the intensity of applied stress. Since the chukars were pen-reared birds, they were in effect subjected only to the stress of starvation, while the Huns and cottontails were subjected to the double stresses of starvation and caging. The Huns were extremely wild, while the chukars did not show any signs of nervousness or restlessness on being caged. It is possible that if a second stress were applied to the chukars, their resistance might be lower.

The relatively large weight loss and the sharp decline in body temperature in only 7 days of stress suggest that the Hungarian partridge were affected markedly by the applied stress, at least in this brief period. A bird of this size, then, which suffers weight and temperature losses of such magnitude, might not be able to survive extremely rigorous winter conditions if it had to go without food for even a relatively short period of time. Huns in the wild, therefore, that were not properly nourished, although not actually starving, could be expected to succumb within a relatively short period of time when exposed to a severe secondary stress such as adverse weather conditions.

Furthermore, with so short a survival time in early spring, presumably the period of greatest resistance to stress according to the information obtained for the hen pheasant (*ibid.*), the Hungarian partridge might be expected to have very low stress resistance and short survival time in early summer, following the natural stresses of the reproductive season.

One experiment in only one month of the year does not, of course, give a complete picture of stress resistance and survival in any of the three species. Further tests performed at different seasons of the year would be necessary to obtain this type of information. The studies reported here, especially in light of the information obtained on hen pheasants throughout the year, indicate that further research on stress response and survival time is warranted on these and other wildlife species, at different seasons and in different years, as another approach toward interpreting wildlife-population behavior.

SUMMARY AND CONCLUSIONS

Groups of Hungarian partridge, chukar partridge, and cottontail rabbits were each subjected to an artificial stress of caging and starvation for periods varying in length from 10 to 12 days. The results of these experiments showed the amount of weight loss and the survival time of these species, and thus indicated their resistance to an applied stress. Although direct comparisons of stress response and survival between species could not be made due to differences in the source of the experimental animals and the month in which the experiments were run, a few general inferences were drawn showing the possible interpretations of these types of data and the need for further research.

LITERATURE CITED

KABAT, CYRIL, R. K. MEYER, KENNETH G. FLAKAS, AND RUTH L. HINE. 1956. Seasonal variation in stress resistance and survival in the hen pheasant. Wis. Conservation Dept., Game Mgmt. Div., Tech. Wildl. Bull. No. 13:1-48.

SELYE, H. 1949. The general-adaptation-syndrome and the diseases of adaptation. *In* Textbook of Endocrinology. Montreal Acta Endocrinologica, Inc., pp.837-867.

Received for publication August 1, 1956.

FOOD OF SEA OTTERS AND HARBOR SEALS AT AMCHITKA ISLAND

Ford Wilke

Branch of Wildlife Research, U.S. Fish and Wildlife Service, Seattle 15, Washington

Studies of the food of sea otters (*Enhydra lutris*) have, because of the limited populations and stringent prohibitions against killing the animals, been necessarily restricted to scat examinations. Scat analyses published by Murie (1940), Williams (1938), and Jones (1951) were alike in showing sea urchin, (*Strongylocentrotus drobachiensis*), mussel (Mytilidae), chiton (Polyplacophora), crab (Anomura and Brachyura), and limpet (Acmaeidae) as the dominant food items. Because of the method of feeding and the relative proportion of hard and soft parts, both scat and stomach examinations often do not accurately represent the relative importance of certain food species. For example, the shell of the rock oyster, *Pododesmus macroschisma*, is usually discarded, and the soft parts of limpets are also extracted from their shells. By contrast, small sea urchins and mussels are simply crunched, shell and all, and swallowed. Large sea urchins may be cracked by beating on a hard surface, but much of the rather fragile shell is swallowed. Miss Fisher (1939) stated that the internal structures of a sea urchin are sucked or licked out after a hole is bitten in the test. Such behavior is not usual when the otters are feeding on the small sea urchins that predominate on Amchitka Island.

In captivity, sea otters crack clams by beating them on any available hard surface to make the soft parts accessible, and some fragments of the shell may be swallowed when the body is eaten. Clams do not appear to enter the diet of sea otters in the wild to any appreciable extent. It is not known whether or not sea otters have the ability or inclination to dig clams from a mud or gravel bottom. It appears that their feeding is confined to species that lie on the bottom or are attached to the surface of rocks and marine vegetation.

In Table 1, giving the stomach contents of five otters, the same food species appear as in the scat analyses. Sea urchins and mussels are most important. The extent to which sea otters feed on fish is not fully known. A fringed greenling appeared in one of the five stomachs, and occasionally a collection of scats may be made up largely of fish bones. There is some evidence that fish are eaten more frequently in the winter and early spring, when feeding conditions are less favorable.

In Alaska, the harbor seal (*Phoca vitulina richardi*) is the subject of more intensive control measures than any other predator. These measures are mostly confined to the mouths of important salmon rivers where the seals feed primarily on eulachon (*Thaleichthys pacificus*) in the spring months but take salmon as the season advances (Heintzlemann, *et al.*, 1954). No stomach-examination results are given in their report to demonstrate how the diet changes. Few harbor seal food studies have been reported for Alaska despite the importance attached to predation by this seal. Imler and Sarber (1947) found that gadids (*Theragra chalcogramma* and *Microgadus proximus*), herring (*Clupea pallasi*), flounders (Pleuronectidae) and salmonids (Salmonidae), in that order, were the leading species taken in southeastern Alaska. On the Copper River during May and June, eulachon was the only food in 64 out of 67 stomachs.

In seven stomachs of harbor seals collected in March on Amchitka Island, octopus was the most frequently taken food (Table 2). Octopus has been reported as a food of harbor seals in localities ranging from Puget Sound in Washington State to Hokkaido, Japan. Gadids, principally Alaska pollack, and crab have appeared in most stomach collections. The fringed greenling is more characteristic of the Aleutian area, where it is very common in inshore waters.

TABLE 1. — STOMACH CONTENTS OF FIVE SEA OTTERS FROM AMCHITKA ISLAND, MARCH 1954

Name of Food Item	Percentage of Food by Volume	Frequency of Item
Starfish (*Asteroidea*)	trace	1
Green sea urchin (*Strongylocentrotus drobachiensis*)	86	3
Hermit crab (Paguridae)	trace	2
Limpet (Acmaeidae)	trace	1
Horse mussel (*Volsella modiola*)	3	1
Mussel (*Modiolaria vernicosa*)	5	1
Fringed greenling (*Hexagrammus superciliosus*)	6	1

TABLE 2. — CONTENTS OF SEVEN HARBOR SEAL STOMACHS FROM AMCHITKA ISLAND, MARCH 1954[1]

Name of Food Item	Percentage of Food by Volume	Frequency of Item
Octopus (*Paroctopus apollyon*)	3	5
Crab (Brachyura?)	trace	2
Alaska pollack (*Theragra chalcogramma*)	trace	1
Cod family (Gadidae)	trace	1
Fringed greenling (*Hexagrammus superciliosus*)	96	1
Unidentified fish	1	1

[1]Two additional stomachs were empty.

The sea otter and harbor seal inhabit the same coastal waters and the rocky beaches and reefs. They provide an example of two fairly large, carnivorous, littoral mammals which are virtually noncompetitive. There is only a slight overlap in their food habits in the same locality. The otter feeds largely on echinoderms and shell-bearing mollusks, whereas the harbor seal depends mostly on free-swimming cephalopods and fishes.

SUMMARY

Five sea otters collected at Amchitka Island, Alaska, in March were found to be feeding on green sea urchin (86 per cent by volume), fringed greenling (6 per cent), mussel (5 per cent), horse mussel (3 per cent), and traces of starfish, hermit crab, and limpet. Seven harbor seals inhabiting the same waters and beaches were feeding on fringed greenling (96 per cent), octopus (3 per cent), and traces of unidentified fish, Alaska pollack, other Gadidae, and crabs. Octopus occurred in 5 of the 7 stomachs. The two littoral mammals are largely noncompetitive in their food habits.

LITERATURE CITED

FISHER, E. M. 1939. Habits of the southern sea otter. J. Mamm., 20:21-36.

HEINTZLEMANN, B. F., I. H. ROTHWELL, AND C. L. ANDERSON. 1954. Alaska Dept. Fisheries Annual Report, No. 6:46-51.

IMLER, R. H. AND H. R. SARBER. 1947. Harbor seals and sea-lions in Alaska. U.S. Fish and Wildl. Serv., Spec. Sci. Rept. No. 28:1-23.

JONES, R. D., JR. 1951. Present status of the sea otter in Alaska. Trans. N. Amer. Wildl. Conf., 16:376-383.

MURIE, O. J. 1940. Notes on the sea otter. J. Mamm., 21:119-131.

WILLIAMS, C. S. 1938. Notes on food of the sea otter. J. Mamm., 19:105-107.

Received for publication October 8, 1956.

SOCIAL AND RANGE DOMINANCE IN GALLINACEOUS BIRDS—PHEASANTS AND PRAIRIE GROUSE[1]

Ward M. Sharp

Pennsylvania Cooperative Wildlife Research Unit, University Park, Pennsylvania

Strife and intolerance are believed to affect the welfare and breeding potential of gallinaceous birds. Information on this phase of population dynamics is meager. Before antagonism can be developed between two or more species of gallinaceous birds, they apparently must be of similar size and form to stimulate the urge to fight or aggression short of fighting. In addition, gallinaceous birds in conflict must occupy the same range, and each must use similar cover types.

Ring-necked pheasants (*Phasianus colchicus*), sharp-tailed grouse (*Pediocetes phasianellus*), and prairie chickens (*Tympanuchus cupido*) were studied on the same range in the Nebraska Sandhills from 1937 to 1943. The author and assistants were in daily contact with these species during the winter and early spring months. Each winter a feeding station maintained near the headquarters of the Valentine National Wildlife Refuge served a large population of pheasants, 50-70 sharp-tailed grouse, and 5-10 prairie chickens. This setting afforded the opportunity to witness fighting among all three species on many occasions. The purpose of this paper is to report techniques used in fighting and to state the results of such conflict.

[1] Acknowledgments: The writer wishes to express his special thanks to F. N. Hamerstrom, Jr., Wisconsin Conservation Department, for constructive comments on the manuscript. Grateful acknowledgments are also extended to Daniel L. Leedy, U.S. Fish and Wildlife Service, and Ray C. Carpenter, Pennsylvania State University. Paper No. 78 of the Pennsylvania Cooperative Wildlife Research Unit and School of Forestry. Journal Series No. 2088 of the Agricultural Experimental Station, Pennsylvania State University, University Park, Pennsylvania, on August 22, 1956.

INTERSPECIFIC DOMINANCE AND DISPLAYS

Sharp-tailed grouse were tolerant of other species, but when conflict developed, they were masters of the situation. They were able to dominate both pheasants and prairie chickens. Pheasants could dominate prairie chickens, but prairie chickens were unable to cope successfully with either the sharp-tails or the pheasants. These statements are based on observed cases of conflict over a period of six years.

During this period of years, ten cases were recorded involving combats between cock pheasants and prairie chickens at the winter feeding station, and two cases of fighting between a prairie chicken and a cock pheasant were observed on the booming territories of the prairie chickens. In these cases of conflict on the booming grounds the pheasant was the aggressor, going out to promote the fight. Eighteen cases were recorded of fights in which a cock pheasant and a sharp-tailed grouse were involved. The sharp-tails were victorious in all engagements with pheasants, while the prairie chicken always lost the fight to a pheasant. Sharp-tailed grouse and prairie chickens were observed on occasion to engage in sparring encounters at the winter feeding area, but the victorious sharp-tail appeared to consider it a playful affair. Conflicts between the two species of prairie grouse appeared to consist only of the establishment of a peck order among

their own kind. Both species of grouse would be seen feeding together within an hour following a tussle.

Each of these species has a characteristic fighting style and form prior to and during combat. The pre-attack posture of sharp-tailed grouse is very similar to its dancing form. The body is slightly crouched and tipped forward; the head and neck extended, paralleling the ground; the wings slightly spread; and the tail held rather erect. From this position, a sharp-tail may dart out at an adversary in combat, or shuffle into its dance on the mating grounds. The male pheasant assumes a fighting posture in much the same manner as that of the domestic rooster or gamecock. It may pick at objects on the ground, circle or feint its opponent for an opening, then it suddenly charges, jumping up and striking its adversary with long, strong legs and sharp spurs. The style of the prairie chicken is identical to that of the pheasant except that it is clumsy and displays awkward footwork. Its short legs and lack of well-developed spurs render it quite ineffective in encounters with pheasants.

An encounter between a pheasant and sharp-tail starts with each bird assuming its typical pre-attack posture. The pheasant feints from side to side; the sharp-tail, set in its crouched position, may take very short steps toward the pheasant. Suddenly the two attack—the pheasant jumping up in typical cock manner to set his spurs; the grouse—in a very low crouch—quickly darting beneath the pheasant and coming up from behind to grasp the ring-neck's tail or rump. Having secured a firm bill-hold on the feathers, it hangs on doggedly. This sudden, unexpected turn of events apparently frightens and intimidates the pheasant, which struggles frantically trying to free itself of the grouse. The pheasant escapes only when the sharp-tail has pulled out all feathers within its grasp or has lost its hold. In cases where the grouse fails to grasp the pheasant, the fight may continue. Seldom did the most aggressive ring-neck make more than three passes at a sharp-tail before the latter was able to seize tail or rump feathers. The pheasant, once defeated, remained clear of any other sharp-tails.

Prairie chickens were most inclined to fight in late winter at the approach of the breeding season; at this time they would square off at a pheasant in typical rooster fashion. After some sparring, pheasant and prairie chicken would rush together and meet in mid-air. The pheasant was so much faster, inflicting punishment with its spurs, that the prairie chicken would take a very rough flogging before freeing itself from the situation. Being roundly defeated and pummeled, it would run and take to flight at its first opportunity. The cock pheasant would give chase, driving the prairie chicken for a distance.

Sharp-tailed grouse are tolerant toward prairie chickens, both occupying the same range in harmony, even though the former is socially dominant. In early fall and winter, flocking and association of the two are common. The fact that both establish separate mating grounds is a factor contributing to tolerance and harmony during the breeding season when conflict would be more pronounced. The pheasant's aggressive nature, its selection of a territory and its tendency, as indicated below, to pursue for a mile are qualities detrimental to the prairie chicken.

Harger (1956) describd the visit of a cock pheasant to a booming ground in Michigan, where the cock was observed chasing prairie chickens about and from the booming site. None of the birds present attempted to defend their area. I have seen similar instances where pheasants chased prairie chickens—the prairie chicken flying, thus avoiding the pursuing pheasant. Once these prairie chickens had fought with and lost to a pheasant on the winter feeding grounds in Nebraska, they never attempted to hold their own against future attacks. Instead they would fly off 25 to 50 yards and alight. Seldom did a pheasant have the opportunity or inclination to pursue further when sharp-tails were present. An aggressive sharp-tail would take up the fight and promptly put the pheasant in another frame of mind. The prairie chickens observed by Harger probably had been attacked and defeated on previous occasions and were now completely submissive to the pheasant. I have never seen prairie chickens refuse their first fight with a pheasant; but once defeated, they seldom accepted or defended repeated challenges. Had the site observed in Michigan been the dancing ground of the sharp-tailed grouse, I believe that the cock pheasant would have made only one visit to pick a fight. The sharp-tails having worked him over, he would have hesitated before coming to engage in a second encounter.

A cock pheasant will eventually drive all prairie chickens from a meadow or booming area during the spring breeding season. Dr. George B. Saunders and the writer, in May 1938, observed a cock pheasant drive a male prairie chicken more than a mile from its mate. The affair started when the pheasant and prairie chicken engaged in a very brief encounter. The grouse took to flight followed by the pheasant. The prairie chicken alighted at about 200 yards, only to be followed and put to flight. Each time it flew, it was pursued in flight by the pheasant. After several stops and starts, the grouse flew off to the distant hills. The pheasant ceased to follow. The female prairie chicken then followed, flying in the direction taken by the male. Subsequent observations on this meadow revealed that the two prairie chickens had disappeared. This instance of pheasant-grouse conflict occurred on a large isolated meadow valley located at the east end of Pelican Lake on the Valentine National Wildlife Refuge in Cherry County, Nebraska. The area, prior to its first invasion by pheasants in 1936, contained favorite booming grounds of the prairie chicken. Persistent attacks day after day disturbed the normal breeding behavior of the chickens, eventually driving them from long-established booming grounds.

POPULATION CHANGES

Small pockets of prairie chicken range exist in Indiana, Illinois, Michigan, Wisconsin, and Missouri. Extensive areas still exist in the Dakotas and Nebraska. Kansas, Oklahoma, and Texas also are reported to possess some prairie chicken habitat. The more eastern and isolated remnant localities represent the eastern and northeastern periphery of the tall-grass prairie. The more extensive western localities represent the western periphery of the tall-grass prairie of the Northern Great Plains where it blends into the drier short-grass region. Here to the west much of the area is not conducive to a high pheasant population, except where cultivation of farm crops is practical and where habitat changes are subjected to drastic shifts from poor pheasant to good prairie grouse years. Years of drought (1932-42) favored the pheasant and disfavored the prairie grouse, but we cannot discount the fact that prior to introduction of the pheasant, prairie chickens seemed to weather both dry and wet periods of the climatic cycle.

There is some evidence that, when a pheasant population invades the range of the prairie chicken, the chickens wane and may cease to exist. Prairie chickens showed a drastic decline on their former booming grounds in the Nebraska Sandhills during 1936-43 when the pheasants became common. When a change in habitat conditions occurred, starting in 1943, the pheasant population crashed (Sharp, 1953). Prairie chickens then increased beyond all expectations and, by 1954, they were just about as abundant as in years prior to 1929. Although this in itself is not conclusive proof of a cause and effect relationship in changing populations of pheasants and prairie chickens, many local observers who were in daily contact with both species believed that the return of the prairie chickens had much in common with the waning of the pheasants.

There are many factors influencing game-bird populations, and these same factors may in turn affect rodents or other associated species. During prolonged drought periods on the Great Plains (1932-42) (Nicholas, 1950), jack rabbits (*Lepus townsendii*) and pheasants were stimulated to successful reproduction in the Nebraska Sandhills. When the wet cycle returned (1943-54), rabbit and pheasant populations dropped, but these same wet years created conditions favorable for the prairie grouse. It is apparent that gallinaceous bird populations are influenced by climatic factors. There is some evidence also that an exotic galliform may effect changes in numbers or distribution of a native galliform regardless of favorable or unfavorable conditions that exist because of climatic cycles.

In order to understand what has happened in Nebraska since the pheasant was introduced, let us go back to the years prior to 1929. Laws were lax, and even local residents shot prairie chickens without much regard to future supplies. The birds' population held up, and no one was particularly apprehensive of any drastic drop in numbers. Since 1930, people have become quite conservation-minded toward "their chickens." And today local residents, living on the western periphery of the prairie grouse range, have very little interest in shooting—even in areas where grouse have been plentiful since 1950.

Severe competition is known to exist between pheasants and prairie chickens, especially during the spring and early summer months when cock pheasants are actively defending their territories. This factor alone could eventually eliminate existing isolated pockets of prairie chickens. But the issue is a very controversial one among (1) the younger hunters, who would rather have only pheasant shooting; (2) the prairie grouse shooters, who prefer their "chickens"; and (3) the conservation-minded few, who desire to dedicate at least a few acres of our rich domain to the prairie chicken.

Strife created by the social and range dominance complex presents a serious problem on areas where conservationists are trying desperately to save even a remnant population of the prairie chicken.

SUMMARY

Observations were made on strife and intolerance within a mixed population of ring-necked pheasants, greater prairie chickens, and sharp-tailed grouse in the Nebraska Sandhills from 1937 to 1943. These species were observed during the winter and early spring months. Techniques used in fighting were observed and the results of such conflict were recorded.

Sharp-tailed grouse were able to dominate both pheasants and prairie chickens, and their success was due to a fighting style unlike that of pheasants or prairie chickens. Pheasants could dominate prairie chickens but the prairie chicken was unable to cope successfully with either the sharp-tails or the pheasants. Fighting form in pheasants and prairie chickens was identical. Sharp-tailed grouse, although socially dominant, were tolerant toward the prairie chicken.

Severe competition existed between pheasants and prairie chickens, especially during the spring and early summer months when male pheasants were defending their territories. This competition could eventually eliminate isolated pockets of prairie chickens in the states where they exist.

LITERATURE CITED

HARGER, ELSWORTH M. 1956. Behavior of a ring-necked pheasant on a prairie chicken booming ground. Wilson Bull., 68(1):70-71.

NICHOLAS, EARL E. 1950. Local climatological summary, Valentine, Nebraska. U.S. Dept. Commerce, Washington, D.C. 6pp.

SHARP, WARD M. 1953. A reevaluation of plant communities within the pheasant range in the Nebraska Sandhills. Ecology, 34(4):771-777.

Received for publication October 10, 1956.

A MARSH DEER "DIE-OFF" IN LOUISIANA

Leslie L. Glasgow and Allan Ensminger

School of Forestry and Agricultural Experiment Station, Louisiana State University, Baton Rouge; and Louisiana Wild Life and Fisheries Commission, Rockefeller Refuge, Grand Cheniere, Louisiana

Although deer "die-offs" due to starvation have been recorded from many upland areas of North America, to the writers' knowledge none has been reported from marsh habitats nor from the state of Louisiana. The following report is presented because of the increasing interest in deer mortality in the Southeast and because of the unique circumstances encountered in the present investigation.

A few reports of marsh deer (*Odocoileus virginianus mcilhennyi*) mortality were received in the fall of 1953, and many were received through the summer and fall of 1954 from the coastal marsh in south-central Louisiana. The critical deer range was located between White Lake and Marsh Island and comprised approximately 400,000 acres adjacent to the Gulf of Mexico in Vermilion and Iberia parishes. The part of this area that we investigated consisted of approximately 100,000 acres south of Intercoastal City.

Most of this marsh was 1 to 2 feet above mean Gulf level, with scattered ridges elevated to 3 feet. With normal tides, prior to the digging of canals, this area was a fresh-water marsh; however, an extensive canal system has permitted the intrusion of salt water and the conversion of some parts of the area to brackish-marsh communities. The area has an average annual rainfall of about 58 inches, an average January temperature of 54°F., an average July temperature of 82°F., and a growing season of 290 days. The normal tidal fluctuation is about 18 inches.

Widespread canal digging, which began in 1925, has continued to the present time. Most early canals were dug for drainage and transportation, with a few being constructed to confine cattle that had grazed the marsh for many years. During the last few years, there has been much oil activity in the area. Since all wells have been drilled from floating barges, canals were required for this work. After extensive canal digging, deer became more numerous, probably a direct result of the increased acreage of elevated land and the drainage of adjacent marshland that provided better deer range than the marsh proper.

Before 1938, the ridges in the area were cultivated and planted to cotton and corn. Since that time no farming has taken place, and the land has reverted to natural marsh conditions, although drainage left these ridges drier than they formerly were. The incidence of anthrax, which periodically plagued cattle (and probably deer) in the marsh, was reduced in seriousness by the vaccination of cattle. Small, interspersed tracts of privately owned land were incorporated with large landholdings, with a consequent reduction in the illegal killing of deer. These factors undoubtedly contributed to the increase of the deer population.

The land has always been trapped and hunted. It has at various times supported high muskrat (*Ondatra zibethica rivalicius*) populations and more recently a high nutria (*Myocastor coypus*) population. Huge flocks of blue and snow geese (*Chen caerulescens* and *C. hyperborea*) winter in the area annually. Severe "eat outs" have been caused in the past by muskrats and geese, with less severe ones recently by nutria. Scars from these "eat outs" still remain in the form of dense stands of annual plants such as marsh fleabane (*Pluchea purpurascens*).

The elevation of the marsh floor with its associated ecological influences is one of the major factors controlling plant types. Often a difference of two or three inches in elevation is sufficient to limit types. The principal elevations and their major plants were as follows:

1. Canal banks
   (a) Pure roseau (*Phragmites communis*)
   (b) Bermuda grass (*Cynodon dactylon*), marsh-elder (*Iva frutescens*), and winter willow (*Baccharis halimifolia*)
   (c) Brush and scattered trees—dewberry (*Rubus* sp.), wax-myrtle (*Myrica cerifera*), yaupon (*Ilex vomitoria*), hackberry (*Celtis laevigata*), honey-locust (*Gleditsia triacanthos*), rattlebox (*Daubentonia texana*), and a variety of plants including deer pea (*Vicia ludoviciana*);

2. Intermediate elevations
   (a) Pure hogcane (*Spartina cynosuroides*)
   (b) Wiregrass (*Spartina patens*), Olney three square (*Scirpus olneyi*) and cocograss (*Scirpus robustus*);

3. Lower elevations
   (a) Cattail (*Typha* spp.), bulltongue (*Sagittaria* spp.), and bullwhip (*Scirpus californicus*)
   (b) Olney three square.

Several other plants occurred on each area but they usually made up a minor part of the plant community except on disturbed areas where annuals such as millet (*Echinochloa* spp.) formed pure stands. Visits to this area in 1950 and 1951 revealed that cattail and saw-grass (*Cladium jamaicense*) were widely distributed in dense stands over the area, but at the time of this study both had practically disappeared.

FIELD INVESTIGATION

During the present investigation, conducted by personnel of the Louisiana Agricultural Experiment Station and the Louisiana Wild Life and Fisheries Commission, 24 deer were found dead. Nine additional animals in late stages of starvation were collected for autopsy by veterinarians in the Louisiana State University Department of Veterinary Medicine. Many dead deer that could not be checked were reported by men employed in the marsh.

Characteristics of the die-off were as follows: (1) there was a marked deterioration in the physical condition of the deer; (2) the animals became listless, permitting humans to approach them quite closely before making a half-hearted attempt to escape; (3) groups of deer were attracted to small areas containing palatable food; (4) weakened animals that were pursued soon became exhausted and were easily caught; (5) weak deer that concentrated along bodies of water were usually found dead near the same location.

DISCUSSION

During the early stages of the "die-off" in 1953, workers in the marsh reported seeing weakened and dead bucks along canals, but rarely reported a weak doe or fawn. It was not until the summer of 1954 that weak does and fawns were commonly seen and later found dead. The field studies, which supported these reports, showed that the bucks died first, does second, and fawns last. This was in the reverse order of mortality for northern "die-offs" which were due to malnutrition (Dahlberg and Guettinger, 1956). At least 90 per cent of the marsh deer's diet was obtained by grazing; therefore, the necessity to reach high for food did not exist in the marsh. Animal nutritionists (Morrison, 1948) have shown that the males of several species require greater quantities of food to maintain bodily functions than females or young animals. They have also shown that females require greater quantities of food than young animals. Assuming that these assertions are correct, one would expect the above-described death pattern on a coastal deer range where there was an inadequate food supply.

As shown in Table 1, 4 dead fawns and 29 dead adult deer were examined, giving an age ratio of 14 young per 100 adults. The sex ratio of dead animals was 182:100. Sex ratios of live deer were not compiled, but since a buck law prevails in the area, it is probable that there were more females present on the range than males and that the actual percentage of the total bucks that died in the herd was far greater than the percentage of does.

The veterinarians' autopsies failed to reveal any causative pathogenic organisms. Cultures were made of major tissues and their blood. In all animals there were congested areas in the lungs, the bladder of each animal was enormously distended, and there was pronounced edema. The three veterinarians agreed that the ailment was of long standing and that the above symptoms were probably of a secondary nature. They suggested malnutrition as a possible cause of the trouble.

TABLE 1. — AGE AND SEX OF DEER FOUND DEAD AND THOSE COLLECTED FOR AUTOPSY

Age (Years)	Sex			Total Animals
	M	F	Unknown	
½	2	2	0	4
1½	7	3	1	11
2½	5	4	1	10
3½	2	1	0	3
4½	2	0	0	2
7½	1	1	0	2
8½	1	0	0	1
Totals	20	11	2	33

During the field investigations it was evident that there was a lack of suitable forage plants. Some plant species had been killed or reduced in vigor primarily by salt-water intrusion and drouth. Before the construction of canals, fresh water was retained over the marsh for prolonged periods following rains. The canals now not only permit the rain water to run off rapidly but also allow salt water to enter the marsh, especially with a moderate to high south wind, which has more influence on tides than the position of the moon and sun. Therefore, interaction between rainfall and wind govern the degree of salinity in the area.

The investigators were not present in the area during 1952 when a drouth accompanied by occasional high tides extended from the latter part of August through October. It is probable that at this time water containing 5,000 to 7,000 p.p.m. of chloride was driven over the marsh by strong winds. In 1953 a drouth extended from late August through September. In 1954 a prolonged drouth occurred with rainfall considerably below normal in every month except July (U.S. Weather Bureau, 1952, 1953, 1954; U.S. Corps of Engineers, 1952, 1953, 1954a, 1954b).

Following the 1952 inundation with salt water, numerous reports were received from marsh landowners of the disappearance of saw-grass and cattail stands. This decrease continued until both plants were almost exterminated over thousands of acres.

Many acres of marsh remained in a dry or stagnant condition with much of the vegetation making very little or no growth in 1954. Deer pea, as well as other succulent plants such as millet, spike rush (*Eleocharis* spp.) and bacopa (*Bacopa caroliniana*), which normally provide large amounts of forage for deer, were almost completely absent. Other plants that supply deer with food became dry and hard early in the spring and failed to produce succulent growth during the entire season. A range survey in the fall of 1954 revealed that there was practically no suitable food or drinking water available for deer. This condition prevailed prior to and during the period when the greatest number of

weak and dead deer were observed. Nutria, geese, and cattle, which were present in the area, competed directly with the deer for food.

Mosquitoes may have contributed to the poor condition of the deer, since unusually large dark clouds of the insects could be observed almost anywhere in the marsh.

Field examinations of dead deer ruled out screw worms (*Cochliomyia* sp.) as a cause of death. Laboratory autopsies suggested that disease was not the primary cause. The very evident symptoms of malnutrition plus the extremely poor condition of the range indicated that the "die-off" was probably a result of malnutrition due to the scarcity of nutritious food.

In the spring of 1955, rainfall, which again became normal, and an intensive burning program were followed by a lush sprout growth of perennial plants as well as many annuals. It was at this season that the surviving deer began to acquire a normal, healthy appearance.

Summary

A study was made of marsh deer mortality in south-central Louisiana in 1953 and 1954. Strong southerly winds inundated the deer range with saline Gulf water in 1952 at a time of severe prolonged drouth. The salt water and drouth eliminated practically all the succulent fresh marsh vegetation on which deer relied for food. This vegetation remained in a stagnant condition through 1953 and 1954. The death of adult male deer in 1953 was followed by the death of additional males plus does and fawns in 1954. Twenty-four dead deer were examined in the field, and nine weakened animals were autopsied in the Veterinary Science Department at Louisiana State University. Disease symptoms were lacking, but symptoms of starvation were very evident. Because of the lack of nutritious range plants, it is believed the "die-off" was due to malnutrition.

Literature Cited

Dahlberg, B. L. and R. C. Guettinger. 1956. The white-tailed deer in Wisconsin. Wis. Cons. Dept., Tech. Wildl. Bull, no. 14:1-282.

Morrison, F. B. 1948. Feeds and feeding. 21st ed. Morrison Pub. Co., Ithaca, N.Y.

U.S. Corps of Engineers. 1952, 1953, 1954a. Salinity charts, Mermentau River, Louisiana. Office of District Engineer, New Orleans, La.

———. 1954b. Stages and discharges of Mississippi River and tributaries and other streams and waterways in the New Orleans Dis'rict. U.S. Corps of Engineers, New Orleans, La. 300pp.

U.S. Weather Bureau. 1952, 1953, 1954. Climatological data, Louisiana annual summary, vol. 57, no. 13; vol. 58, no. 13; and vol. 59, no. 13.

Received for publication September 19, 1956.

CROP THICKENING AND SEPTEMBER NESTING OF DOVES

Larry D. Caldwell

Department of Zoology, University of Georgia, Athens

It is generally accepted that the presence of pigeon milk in the crop of an adult dove indicates that it has dependent young. However, Peters and Wolfe (1954) state that the relationship between "glandular" crop thickening and nestling dependency has not been satisfactorily determined. Little evidence has been presented to date to show that crop thickening is a reliable indicator of nestling dependency, yet the thickened crop is one of the criteria used in determining opening dates for hunting seasons.

During the second and third weeks of September 1954, 36 adult mourning doves (*Zenaidura macroura*) were collected in southern Michigan. The collections were made within ten miles of the Michigan State University Kellogg Bird Sanctuary and Farm where an intensive dove-nesting study was being conducted by the author (Caldwell, 1955). Of the 36 adults collected, 15 (42 per cent) had thickened crop walls, and four others showed a trace of the thickening. Eighteen of these 36 adults were taken under hunting conditions over fields having flocks of from 7 to 45 birds. The incidence of crop thickening in these adults was 39 per cent. Only four (10 per cent) of an observed 41 pairs of breeding doves on the Sanctuary and Farm were nesting in September and thus might be expected to have the thickened crop. Two of these pairs fledged their young before September 8. Since the percentage of the occurrence of the thickened crop in the sample of collected birds was so high, it seems that either the sample was unconsciously biased in favor of doves with a thickened crop or, as also seems likely, the thickened crop in a September adult does not necessarily mean that it is still nesting.

Hamm (1948) reported that 17.8 per cent of 1,187 adult doves shot in eastern Tennessee in September were feeding young as judged by crop conditions. Korschgen (1955) reported that 6.0 to 6.8 per cent of 1,359 September-shot doves examined in Missouri in 1951-53 had thickened crops. Quay (1951) reported that 20.5 per cent of 278 adult doves in North Carolina examined during September in 1939-41 had pigeon milk in their crops at a time when 24 (13 per cent) of 184

observed (eventually successful) nests were not yet completed. In Georgia, Jenkins (1955) found that 35 per cent of 79 adults collected in September had thickened crop walls, yet Hopkins and Odum (1953) working in the same area could find very few active nests in September (for example, only one out of 31 nests studied in 1951 was still active in September). Jenkins concluded, however, that a definite shooting bias existed under the collecting conditions. It would appear from these data that the presence of a thickened crop as determined by superficial examination of birds in hunters' bags may not be a reliable indicator of September nesting. Further studies of the crop condition of September nesting adults are needed to clarify this matter.

LITERATURE CITED

CALDWELL, LARRY D. 1955. A nesting study of the mourning dove in Kalamazoo County, Michigan. M.S. thesis, Michigan State University Library, East Lansing. 44pp.

HAMM, HALLIE. 1948. Dove survey results. Tenn. Coms., Jan.-Feb., 4pp.

HOPKINS, MILTON N. AND EUGENE P. ODUM. 1953. Some aspects of the population ecology of breeding mourning doves in Georgia. J. Wildl. Mgmt., 17:132-143.

JENKINS, JAMES H. 1955. A contribution to the physiological ecology of the mourning dove *Zenaidura macroura carolinensis* (Linnaeus). Ph.D. thesis, University of Georgia Library, Athens. 100pp.

KORSCHGEN, LEROY J. 1955. A study of the food habits of Missouri doves. Missouri P-R Report 13-R, 31pp.

PETERS, HAROLD S. AND JOAN H. WOLFE. 1954. Mourning dove newsletter No. 8, U.S. Fish and Wildl. Serv., 9pp.

QUAY, THOMAS L. 1951. Mourning dove studies in North Carolina. N. C. Wildl. Res. Comm., Fed. Aid Project 2-R and 26-R, 90pp.

Received for publication October 18, 1956.

VALIDITY OF SPUR LENGTH AS AN AGE CRITERION IN PHEASANTS

Allen W. Stokes

Department of Wildlife Management, Utah State Agricultural College, Logan, Utah

Measurement of the length of a particular body structure is a common method of distinguishing between adults and juveniles in a wide variety of animals. Structures most commonly used by game biologists are baculum (Elder, 1951; Sanderson, 1950); incisor width (Sooter, 1946); bursal depth (Hochbaum, 1942; Linduska, 1943); and length of spurs. An ideal age character is one with no overlap in lengths of adult and juvenile structure. With most age criteria, however, there is a certain degree of overlap in measurements, hence the usual inability to use weight, limb length, or body length.

Earliest attempts at aging pheasants (*Phasianus colchicus*) involved largely qualitative characters. Adults were separated from juveniles on the basis of length, shape, color, hardness, and texture of the spur (Linduska, 1943, 1945). Linduska believed that by such methods juveniles might be distinguished from adults with a high degree of accuracy. Subsequent investigators, however, believed that these largely qualitative characters were unreliable when applied extensively, and have turned to a quantitative character—spur length.

Linduska (1943) first proposed spur length as an age character for pheasants. He plotted the distribution of spur lengths of 337 cock pheasants, the age of which he determined by bursal examination. There was very little overlap between adult and juvenile spur lengths; but to distinguish between adults and juveniles from inspection of the curve alone would have been difficult (Fig. 1). Linduska's sample of spurs was atypical. It came from a population in which the ratio of juveniles to adults was 23:1. The juvenile portion of the curve almost completely dominated the adult portion. In most pheasant populations, where cocks only are

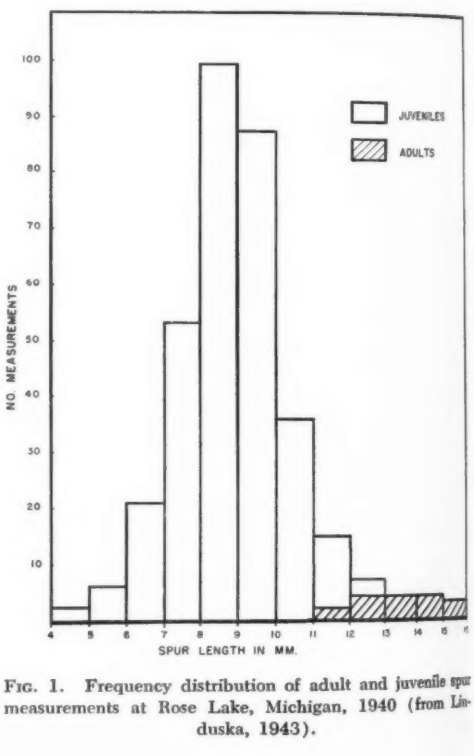


FIG. 1. Frequency distribution of adult and juvenile spur measurements at Rose Lake, Michigan, 1940 (from Linduska, 1943).

shot, cock age ratios vary from 3 to 20 juveniles per adult. Fig. 2 gives the distribution of spur lengths from samples collected in four different states. Age ratios of these samples varied from 2.4 to 3.0 young per adult. The strongly bimodal distribution that one looks for in an age criterion to separate adults sharply from juveniles is conspicuously lacking in these curves. One cannot distinguish between adult and juvenile spurs by inspection of these curves alone.

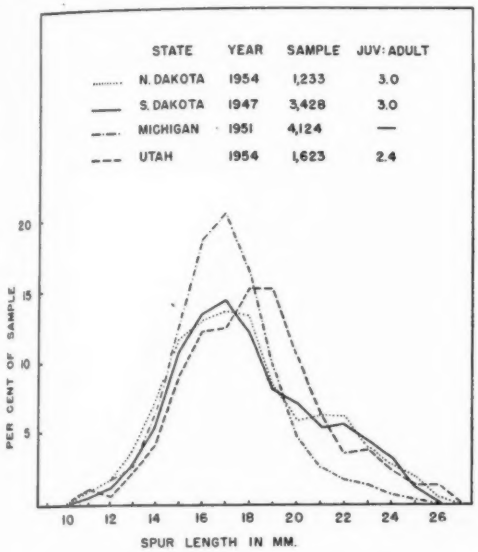

STATE YEAR SAMPLE JUV: ADULT
N. DAKOTA 1954 1,233 3.0
S. DAKOTA 1947 3,428 3.0
MICHIGAN 1951 4,124 —
UTAH 1954 1,623 2.4
PER CENT OF SAMPLE
SPUR LENGTH IN MM.

FIG. 2. Distribution of spur lengths from pheasants shot in hunting season.

Kimball (1944) proposed the use of a gauge of such diameter that it would pass over the short spur of a juvenile cock pheasant but be stopped by the longer spur of an adult. He realized that there would be some overlap in spur lengths of adults and juveniles. To minimize this error he used a gauge of ¾-in. diameter. With this diameter as many juveniles in his sample would be incorrectly called adults as adults would be called juvenile. Hence, compensated error was zero. After more extended measurements, the diameter of the gauge was increased to 25/32 in. or 19.6 mm. (Nelson, 1948). Kimball recognized that time of hunting season and geographic differences would create differences in spur length. Despite his caution, biologists in some other states have adopted the Kimball gauge as an age criterion with no attempt to modify it for local conditions. To be sure, I have found no age ratios in the literature based upon the Kimball gauge alone. But I have found this practice reported in the *Pittman-Robertson Quarterly Progress Reports* from two different states and have learned of similar practice among other biologists from personal communication. Therefore, it seems well to point out the degree of error that one might encounter by relying strictly upon the Kimball gauge.

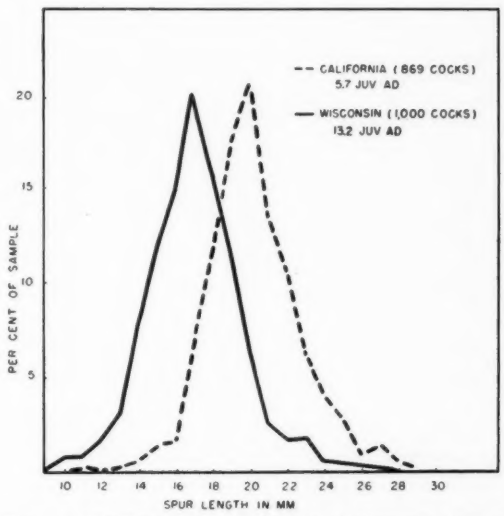


FIG. 3. Distribution of spur lengths of pheasants shot in Sutter Basin, California, and in Wisconsin, 1954.

I wish to thank the following people for furnishing me with samples of pheasant legs used in Figs. 2 and 3: F. H. Wagner, Wisconsin Conservation Department; C. M. Hart, California Department of Fish and Game; W. J. Miller, North Dakota Game and Fish Department; and C. M. Greenhalgh, Utah Fish and Game Department.

SPUR GROWTH

One source of error in the spur gauge lies in the fact that spurs of juvenile pheasants continue to grow throughout the hunting season. Nelson (1948) found that mean spur lengths of juvenile cocks in South Dakota increased on the average of 1.5 mm. in the two months from October 15 to December 13. For 40 captive juvenile cocks that I studied in Utah, the average growth over a similar period (18 to 27 weeks) was 2 mm., the mean spur length increasing from 17.1 to 19.1 mm. The number of spurs reaching 19.6 mm. in this period increased as follows:

Age of cocks in weeks	16	18	20	22	24	26
Per cent reaching 19.6 mm.	0	5	10	20	33	42

Hence, if a spur gauge of fixed diameter were used throughout a hunting season, more and more juveniles would be misclassified as the season advanced. Differences in the interval between hatching and hunting season will also affect average spur length and influence the accuracy of the spur gauge. At onset of hunting in 1954, cock pheasants in California were about eight weeks older than those in Wisconsin as indicated below (data furnished by C. M. Hart and F. H. Wagner):

	California	*Wisconsin*
Peak of hatching	June 1	June 20
Start of hunting	November 20	October 16
Age at hunting (weeks)	25	17

The difference in distribution of spur lengths for these two states is shown in Fig. 3. The peak of spur distribution occurs at 20 mm. for the California sample and at only 17 mm. for Wisconsin. On the basis of growth rates of spurs reported above, about half of this 3-mm. difference is probably attributable to the greater age of the California birds at the time of the hunting season. Use of the Kimball gauge on this California sample would give an age ratio of 0.66 young per adult. Actual age ratio of this group of cocks, as determined by bursal examination, was about 5.7 young per adult based on a sample of 537 cocks taken from the same area (Hart, pers. comm.). Hence, use of an unmodified Kimball gauge in California would be highly unsatisfactory. Hart believes a gauge of about 22 mm. would be necessary for California birds.

Some of the differences between California and Wisconsin spur lengths may be due to differences in strain of pheasants, but there have been no studies to confirm this.

FLUCTUATION IN AGE RATIOS

Variable fall age ratios also affect spur-length distributions. Kimball's spur gauge was designed to give 100 per cent compensated accuracy in an area where fall age ratios of cocks were approximately 3 young per adult. Figures in Table 1 come from data presented by Berner (1947). To show the effects of age ratios, I have multiplied the young segment of his sample in one instance by 2 and in another instance by 5 to create samples with age ratios of 6 and 15 young per adult respectively. With an age ratio of 6:1, the spur gauge would have to be increased to 20.0 mm. to give the true age ratio of this sample. Similarly, with an age ratio of 15:1, a gauge of 20.4 mm. would be necessary. If the standard gauge were used, the true age ratios would be considerably in error, as shown in the final column of Table 1.

Fluctuations in fall age ratios of the degree shown in Table 1 may occur from one year to the next within any state. Similarly wide fluctuations may occur between areas of high and low productivity within a state and between states.

TABLE 1. — THE EFFECT OF VARIABLE COCK AGE RATIOS IN THE POPULATION ON DETERMINATION OF COCK AGE RATIOS FROM SPUR LENGTHS

True Age Ratio (Young per Adult)	Diameter of Gauge Required to Give Correct Age Ratio (mm.)	Calculated Age Ratio Using 19.6-mm. Gauge (Young per Adult)
3.0	19.6	3.0
6.0	20.0	4.4
15.0	20.4	10.9

The above sources of error are so great that the Kimball spur gauge should not be used without making corrections for (1) regional differences in spur lengths of pheasants, (2) age in weeks of pheasants when shot, (3) changing age ratios from year to year or from one region to another. Few of these corrections can be made unless a large sample of spurs is available and can be checked against bursal depths.

CONCLUSION

Perhaps because of the difficulty of correcting for the above sources of error in the spur gauge, biologists in many states have now virtually abandoned this technique. Instead, they are reverting to the very same qualitative spur characters for determining age recommended 12 years ago by Linduska (1943). Where biologists can run through a long series of pheasant legs of known age, it seems possible for them to learn how to distinguish juveniles from adults with considerable accuracy. There are as yet no published reports on reliability of this method. It has the weakness of subjective judgment and qualitative rather than quantitative standards—a weakness the spur gauge was supposed to eliminate. Hence, aging of pheasants has swung full circuit and has now returned to the general methods in use 12 years ago. That this method approaches the accuracy of the bursal-depth technique is questionable. It is hoped that biologists using qualitative spur characters will publish their results promptly for the benefit of newcomers to the field.

LITERATURE CITED

BERNER, LESTER M. 1947. Bag check of South Dakota's pheasant hunters—1947. S. D. Pittman-Robertson Quart. Rept., 9:16-42.

ELDER, WILLIAM H. 1951. The baculum as an age criterion in mink. J. Mammal., 32:43-50.

HOCHBAUM, H. ALBERT. 1942. Sex and age determination of waterfowl by cloacal examination. Trans. N. Amer. Wildl. Conf., 7:299-307.

KIMBALL, JAMES W. 1944. Age gauge for pheasants. J. Wildl. Mgmt., 8:263-264.

LINDUSKA, J. P. 1943. A gross study of the bursa of Fabricius and cock spurs as age indicators in the ring-necked pheasant. Auk, 60:426-437.

———. 1945. Age determination in the ring-necked pheasant. J. Wildl. Mgmt., 9:152-154.

NELSON, BERNARD A. 1948. Pheasant data from a two-year bag study in South Dakota. J. Wildl. Mgmt., 12:20-31.

SANDERSON, GLEN C. 1950. Methods of measuring productivity in raccoons. J. Wildl. Mgmt., 14:389-402.

SOOTER, CLARENCE A. 1946. Muskrats of Tule Lake Refuge, California. J. Wildl. Mgmt., 10:68-70.

STOKES, ALLEN W. 1954. Population studies of the ring-necked pheasant on Pelee Island, Ontario. Ontario Dept. Lands and Forests, Tech. Bull. Wildl. Ser. No. 4:1-154.

Received for publication October 1, 1956.

A COLLAR FOR IDENTIFICATION OF BIG GAME[1]

Donald R. Progulske

South Dakota State College, Brookings, South Dakota

All methods yet devised for marking big-game mammals individually have undesirable features. Colored plastic ear tags, as used by Leopold, *et al.* (1951) to mark mule deer (*Odocoileus hemionus*), may be recognized up to one-quarter mile if conditions are optimum and a telescope is used. However, these markers are usually recognizable only at much shorter distances if many different colors and patterns are employed; moreover, they are often lost. Ear cuts used in combination with tags are usually recognizable only at short distances and are sometimes confused with natural deformities. Large areas of dyed pelage can be seen farther, but some dyes fade, and at best they are lost with the molt (Webb, 1943; Clover, 1954). Natural deformities and markings have been used to identify individuals (Kabat, *et al.*, 1953), but often too few animals have distinctive markings. The use of bells enables observers to secure records for many deer that are not seen, but it is possible to mark only small numbers of animals individually with bells (Taylor, 1947 and pers. comm.).

During a study of movements and home ranges of white-tailed deer (*O. virginianus*) in Missouri, the writer developed a conspicuously colored collar that proved superior in some ways to the marking schemes discussed above.

The collar was made of belt leather, "heavy weight" Duran upholstery plastic (obtained from T. Matthews Upholstery Company, Kansas City, Missouri), and a 1-inch buckle, according to the specifications given in Fig. 1. The buckle was attached so that the plastic could be cemented to the rough side of the leather. Goodyear Pliobond cement proved to be most satisfactory for fabricating the plastic design and attaching it to the leather; the plastic was best cemented to the leather when the ends of the collar were buckled together. The plastic and leather sometimes were also sewn together for added strength. Outdoor-exposure tests of the plastic made for one full year indicated that this material is durable, color-fast, and flexible even at below-freezing temperatures. Five colors of plastic (red, yellow, green, black, and white) were used in combination with five designs shown in Fig. 1. In favorable light these designs were eas-

[1] Contribution from the Missouri Cooperative Wildlife Research Unit: U.S. Fish and Wildlife Service, Wildlife Management Institute, Missouri Conservation Commission, Edward K. Love Foundation, and the University of Missouri cooperating.

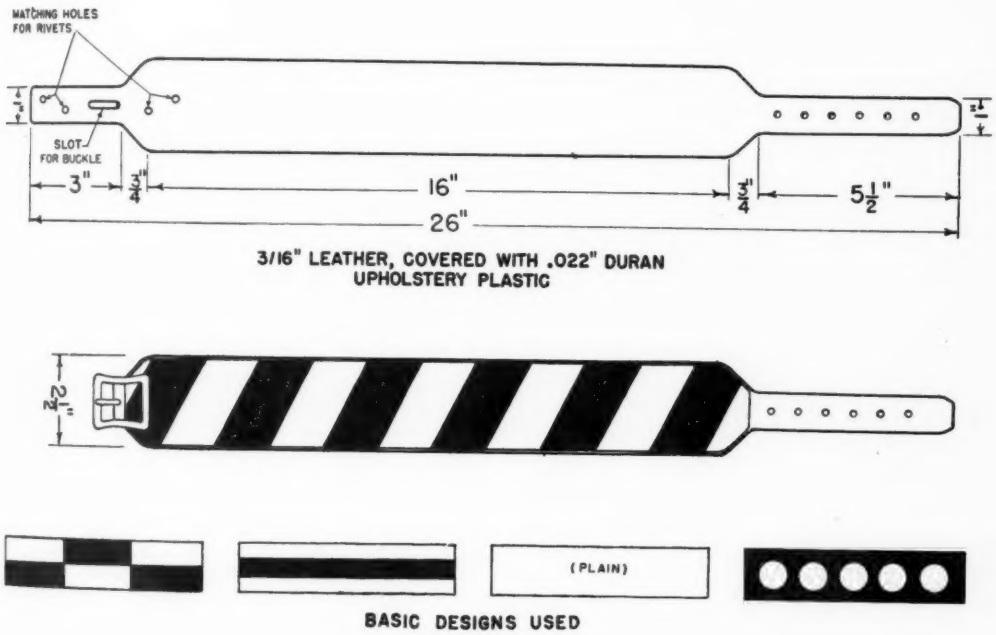


FIG. 1. Specifications for deer collar.

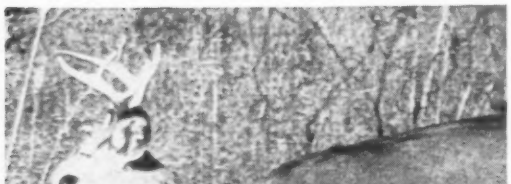


FIG. 2. Adult male white-tailed deer in rut and with swollen neck, marked with collar.

ily identified at 350 yards with the aid of seven-power binoculars. A collared deer is pictured in Fig. 2.

The collars were buckled loosely around the necks of the deer to allow for future growth and swelling of the necks of bucks during the rutting season. The 26-inch collar used in this study formed a circle 20 to 23 inches in circumference when buckled. This size appeared to be adequate for the eight adult bucks and does marked, but one collar that was buckled to the minimum circumference was later found to fit snugly on a 2½-year-old buck. For more accurate information bearing on collar size, measurements were made on the smallest circumference of the necks of adults killed during the hunting season, which, in Missouri, partly coincides with the rut. Measurements of 40 adult males of age classes 2½ through 5½ years ranged from 17 to 31 inches, and averaged 22 inches. The neck of one large female was 16 inches in smallest circumference. From these measurements and the experience with collared deer, a collar 20 to 21 inches in circumference is recommended for females, and one of 25 inches in circumference is recommended for males.

The collar is not suitable for very young deer, because if buckled loosely enough to permit growth, it can slip over the head. Incorporation of an elastic section might solve this problem.

There was no evidence in this Missouri study that these collars ever contributed to mortality by hanging deer up in vegetation or in fences, nor was this trouble encountered when sizable numbers of deer were belled in Texas (W. P. Taylor *in litt.*).

Deer with wide, colored collars were seen for periods as long as 16 months; one was identified 29 times during 6 months. A narrower, uncolored leather collar was helpful in visual identification of a belled deer that was seen 28 times. After 19 months, the deer was shot, and the collar was found still in good condition. No collars applied to yearlings or older deer in this study were known to be lost afield.

All deer provided with collars were also marked with laminated ear tags. These tags were made from two discs of colored acetate plastic 0.015 to 0.020 inch thick, 2½ inches in diameter, and cemented with acetone. A distinctive design with contrasting color was then bonded to the outer face of the laminated disc. These laminated markers were much more durable than those made from a single layer of plastic.

After this note was submitted for publication, the use of reflective collars on Australian mammals was described by Ealey and Dunnet (1956). Their method involved (a) strips of polyvinyl chloride instead of leather as the basic collar and (b) a clever system of symbols used to number individual animals.

LITERATURE CITED

CLOVER, M. R. 1954. Deer marking devices. Calif. Fish and Game, 40(2):175-181.

EALEY, E. H. M. AND G. M. DUNNET. 1956. Plastic collars with patterns of reflective tape for marking nocturnal mammals. C.S.I.R.O. Wildl. Res., 1:59-62.

KABAT, C., N. E. COLLIAS AND R. C. GUETTINGER. 1953. Some winter habits of white-tailed deer and the development of census methods in the Flagg Yard of northern Wisconsin. Wis. Cons. Dept. Tech. Wildl. Bull., no. 7:1-32.

LEOPOLD, A. S., T. RINEY, R. MCCAIN, AND L. TEVIS, JR. 1951. The Jawbone deer herd. Calif. Div. of Fish and Game, Game Bull. no. 4:1-139.

TAYLOR, W. P. 1947. Some new techniques—hoofed mammals. Trans. N. Amer. Wildl. Conf., 12:293-324.

WEBB, W. L. 1943. Trapping and marking white-tailed deer. J. Wildl. Mgmt., 7(3):346-348.

Received for publication September 17, 1956.

REVIEWS

Conserving American Resources. By Ruben L. Parson. Prentice Hall, Englewood Cliffs, New Jersey, 1956. 550 pp. $8.65.

This comprehensive presentation on American resources is compiled and written by a single author, a geographer. This method has the advantage of uniformity of writing and treatment and of good coordination of the many parts. It has the inherent disadvantage that the author cannot be expert in all the fields discussed and may therefore fall into errors of fact or judgment. The alternative is to have an editor bring together chapters by different authors, each expert in his field. This often results in varied style, conflicting opinions and inadequate correlation.

This reviewer prefers the approach used in this book when it is well done, and this one is well done. The author thinks ecologically and thus, even though the subject is necessarily compartmented into chapters, they are well tied together. While wildlife is objectively treated in three chapters, it is frequently discussed in others as wildlife is affected by other resources.

The subject is handled in seventeen chapters. Included are three that set the stage, reveal the author's philosophy, fit conservation of resources into the American social system, and look into our future prospects. They open the book (two chapters) and close it. In between, water is given two chapters, soils and land four, forests two, grasslands one, wildlife (including fisheries) three, recreation one and minerals one. The "unified approach to conservation" is the key theme. Following the subject matter chapters is a section on teaching aids and one on bibliography. It is amply illustrated with 214 photographs, line drawings and charts. The diagrammatic drawings are well done, but some of those depicting scenes in cartoon style are poor. The mediocre paper used in the book impairs the clarity of some of the illustrations.

The three wildlife chapters are titled: "Wildlife: Functions and Abuses;" "Wildlife Conservation;" and "Our Bordering Seas." Wildlife history and problems and the main segments of management are fairly well presented but with a tendency to oversimplify. The protectionist view is given somewhat more emphasis than the sustained-use view. The general wildlife treatment is to discuss conditions and principles. The animals themselves come in mostly in citing examples. Farm wildlife is given more prominence than forest and aquatic species. Proper stress is given to the importance of habitat and land use and the limited places for artificial propagation and restocking, introduction of exotics, winter feeding and control of predators. The slaughter of wildlife in the pre-conservation era is over-dramatized and the extinction of species by man's actions treated with more sentiment than necessary. Predator stomach analyses are used as the whole story in judging their niche; the insect- and seed-eating habits of birds are used to reach incomplete appraisals of their economic value; it is intimated that all land drainage is unwise. Nevertheless, the author has generally kept ecological principles pretty straight and does a good job of showing the complex relationships in wildlife populations.

The chapter on ocean resources also includes what little is given on fresh-water sports fisheries.

This book is suitable as a text for a basic college course in natural resources. The author has also planned it for use of teachers in high school and the upper grades. It is a good book for the layman to read. The author's style is clear and readable with enough humour to provide a bit of spice.

The author is optimistic about our future, a reassuring view but possibly too much so, this reviewer thinks. He places primary stress on education as *the* tool to accomplish conservation. He emphasizes the importance of the generalist in conservation work as contrasted with the specialist. He says that every professional conservator should be thoroughly grounded in geography. These are viewpoints to stimulate vigorous discussion—and they are for him, a teacher of geography, a natural and healthy bias.—FRANK C. EDMINSTER, U.S. Soil Conservation Service, New Brunswick. N.J.

Pelican in the Wilderness. By F. Fraser Darling. Random House Inc., New York. 1956. 380pp., illus. $5.00.

Few people who have any interest in nature or renewable-resource conservation can fail, surely, to find this book of absorbing interest. Written in beautiful English and with frequent change of pace, it takes us with Dr. Fraser Darling, the ecologist, first to UNESCO and IUPN meetings at Lake Success in 1949, then in 1950 through Wisconsin, southwestern United States, Wyoming through to Florida, and to Mexico. Finally we are carried to Alaska, in 1952.

We meet a veritable who's who of United States conservationists—such names, randomly selected, as Paul B. Sears, Warren Weaver, Hugh Bennett, J. J. Hickey, D. I. Rasmussen, Starker Leopold, Olaus Murie, Wm. Albreit, Enrique Beltran, and John Buckley will give some idea of the wide range of interests and areas sampled. Even allowing for these many outstanding contacts, one is still amazed at the wealth of observations made by the author; one comes to realize more fully the experience and mental capacities that have already made him known and respected by many on this continent.

Fraser Darling, then, draws upon a surprising range of interests to weave around his central theme of ecology a kaleidoscopic word picture touching

on architecture, religion, morals, pollution (as in Chicago), bull fighting, hill-billies (sic), and other matters too numerous to mention. He shows a special interest in eating places, and his vivid mention of liver and bacon will stir the memory of many a reader. The multitude of topics commented upon dilutes much of the scientific theme, but makes for an absorbingly interesting and human story.

Drawing upon his experience in his own country, especially in the Scottish Highlands, the author makes pointed comment upon many of our agricultural practices on this continent, particularly as they relate to grazing. Similarly he relates his experience to many of our wildlife range problems. The excellent contribution he makes to our ecological understanding makes one wish that as a people we were more ready to avail ourselves of the experiences of the older nations. At the same time, the author's glowing tributes (well-deserved, too!) to the ability and work of many of our North American conservationists make one wonder if we appreciate what we have at home.

It is perhaps inevitable, but still to be regretted in a book of this kind, that many problems are oversimplified. To the scientist, this is vaguely annoying but not really harmful, as he should have the specialized knowledge to think these problems through. To the lay reader, without the necessary background, a disservice may be rendered. How many of our difficulties in wildlife management have arisen from limited understanding, by the public, of the complexities of our problems. Thus the presentation (with little or no qualification or comment) of such generalities as the realization of ". . . how important the wolf was in the well-being of a herd of deer . . .," that "Annual breeding in the Arctic is not the general rule," that the coyote-control policy in the United States ". . . is already showing its consequences in rodent irruptions in the wake of control," and that "Dave has found that, when shortage of food makes itself felt, the moose stops breeding, a merciful check to over-population which seems denied to many other deer" will cause many a wildlife biologist (and layman, too) more than a little unease. The conclusion drawn that to find men catching, in the Colville River (?), fish two feet long is ". . . some indication of the richness of the environment . . ." will leave fisheries biologists wishing there had been some mention of age of the fish, of their movement patterns and of the fishing pressure, to support the thesis. We have all wished at times that we might reduce our problems to a few simple statements, but bitter experience has taught us that things biological can rarely so be treated. The author, from his deer work and other researches, knows this, and in fact indicates such in this book in his discussions with Errington on self-regulatory thresholds in wild populations. But he leaves the trap set for the unwary reader, with few warning posters to guide him around it.

Other statements in the book may be challenged. For example, all trap lines in Canada are not registered, contrary to the author's informant, the Customs man. Social anthropologists may argue the conclusion implicit in the general statement, relating to the future of Eskimos if thrown from gainful employment once more upon their own resources, that "Salvation will be in the paradox, in that the old hunting life has never been thrown aside, but has remained co-existent with the rubber, the kerosene, and the bread." Certainly northern administrators would like to feel so assured. Archaeologists may wish to quarrel with the statement (unqualified) that the Orkov culture (does he mean Okvik?) has produced the finest eskimo art in Alaska, and that all eskimo cultures since have fallen short of that standard. There appears to be some mistake in calculations relating to Nunivak Island and its caribou populations. Perhaps this is due to a major typographical error; there are unhappily quite a few minor ones.

Finally, the author, who pulls no punches in his comments upon persons, places and things, may hurt a few feelings. This may be unavoidable in a book touching on human ecology. Yet as one reads this book one feels that here is a man of great sympathy and human understanding. Can it be then, that the "harsh word written" is but a cover, the accoutrement of the scientist self-styled ". . . a pessimist philosophically and one content to be a désillusionné"? Readers will have to draw their own conclusions.

In summary, biologists and ecologists will want to read this book. They may expect to find good ecology, good sense, plenty to argue about, and much heart-warming exposition. They will not learn any new principles or find any answers to their problems.—W. WINSTON MAIR, Canadian Wildlife Service, Ottawa, Ontario.

The Future of Arid Lands. Edited by Gilbert F. White. American Association for the Advancement of Science, 1515 Massachusetts Ave., N.W., Washington 5, D.C. 1956. ix + 453pp., 49 illus. $6.75 (AAAS members, $5.75).

From April 26 to May 4, 1955, there assembled in New Mexico a group of authorities to participate in a symposium on the subject of arid lands of the world. This international conference was held under the auspices of the American Association for the Advancement of Science and the Southwestern and Rocky Mountain Division of the A.A.A.S. Major financial backers of the conference were the United Nations Educational, Scientific, and Cultural Organization (UNESCO), the National Science Foundation, and the Rockefeller Foundation. The University of New Mexico at Albuquerque and the New Mexico Institute of Mines and Technology at Socorro served as hosts for the meetings. The interna-

tional nature of the conference is indicated by the fact that representatives of 28 countries were in attendance.

The conference pursued the subject of arid lands under five main headings: The Broad View; Variability and Predictability of Water Supply; Better Use of Present Resources; Prospects for Additional Water Sources; and Better Adaptation of Plants and Animals to Arid Conditions. Under these various headings, 33 papers were presented.

The volume, ably edited by Gilbert F. White, includes these papers, as well as a summary statement by Olaf S. Aamondt and 31 conference recommendations.

For the purpose of this conference, arid lands were considered to include also the semi-arid regions, such as the Great Plains of the United States. The immensity of the arid lands is made clear by the first paper, which points out that on about one-third of the land area of the earth, moisture is the chief factor limiting production of plant growth.

The volume presents a mass of facts and authoritative views regarding the characteristics of arid lands, the adaptations of plants and animals to arid conditions, and the present and possible future economic uses of such lands. The need for research and the organized exchange of information on all phases of the economic development and human use of the products of such lands received prominent attention in several papers and in the recommendations.

Readers of THE JOURNAL will note that practically all of the thinking is directed toward ways and means of encouraging arid lands to produce crops of food, fiber, resins, forage for domestic stock, and other products to meet the demands of an ever-increasing human population. The presentations include ways of providing supplemental supplies of water, the reduction of salinity, the selection and development of domestic plants and animals better adapted to arid land conditions, and human uses of native vegetation that is now being produced on such land.

Little attention is given to the conservation or development of arid lands for recreational use or for the production of wildlife. However, one recommendation (No. 26) reads as follows: "Natural arid land, ecological communities of indigenous animals and plants in their original habitats, are essential for educational and scientific purposes. Areas of adequate size should be acquired and preserved in the various arid land countries." One paper specifically discusses the consequences of using arid lands beyond their capabilities.

Of special interest to those working in the field of wildlife management are the 58 pages composed of seven papers dealing with the adaptation of plants and animals to arid conditions.

The volume is attractively printed on good-quality paper. A good index, as well as lists of reference material for most of the papers, aid in making this volume a valuable reference for those working with the agriculture, soils, climate, plants, economics, or animals, including humans, of the arid regions of the world.—A. E. BORELL, U.S. Soil Conservation Service, Denver, Colorado.

The White-tailed Deer in Wisconsin. By Burton L. Dahlberg and Ralph C. Guettinger. Game Management Division, Wisconsin Conservation Department, Madison 1, Wisconsin. Technical Wildlife Bulletin no. 14. 282pp. 1956.

This book is the first complete report on 14 years of deer research in Wisconsin. For the many who do not have ready access to state publications, it is the first information that has been generally available on the progress of Wisconsin deer management.

The authors must be credited with having done an excellent job of organizing and presenting the material that has accumulated in files during the many years that the Wisconsin deer project has been in operation. The historical section, in particular, is well handled. The presentation of the long struggle to attain successful deer management will be read with sympathetic interest by game managers throughout the land.

The sections on deer food habits and requirements, artificial feeding, and range relationships are perhaps the strongest portion of the book, and obviously represent the major emphasis of the field work. The data presented in these sections will provide useful reference material for all big-game workers.

Criticism must be directed primarily against the population section of the report. It is unfortunate, for example, that in 14 years of study there was not greater effort directed toward obtaining information on deer numbers or population densities. With this information almost completely lacking, it is inevitable that the treatment of other population characteristics would be not entirely adequate. The presentation of population data, lumped for the entire state, gives results of questionable significance, considering the variety of habitat differences and environmental pressures affecting the many populations concerned. The methods of obtaining data on population phenomena in general are somewhat uncritical.

The attempt to study deer movements in Wisconsin, like those in many other states, involved much effort in trapping and tagging deer, but little or none in following up the marked animals. Thus, 898 deer were trapped, but tag returns were received from only 78. With a small expenditure of man power directed toward following marked deer these ratios could perhaps have been reversed, with worth-while information on deer movements resulting. The data on deer mobility available to the writers called forth a maximum of inductive rea-

soning. Some confusion is brought into the discussion by the decision to call the deer nonmigratory, and to treat winter yard and summer range as part of one home range. The inability to distinguish between normal travels of a deer, within a home range, and the more uncommon dispersal travels, rutting-season travels, or occasional wanderings of deer, results from the scarcity of tag returns. There is a need to make more definite distinction in the discussion between the travels of transplanted deer, and the movements of deer within a familiar home area. In general, the information presented in this section of the book can only be properly evaluated when a more adequate study of white-tailed deer movements has been completed.

It is hoped that these specific criticisms will not detract from the credit that the authors deserve for having completed a difficult task. The book is a worth-while addition to the library of anyone interested in deer.—RAYMOND F. DASMANN, Humboldt State College, Arcata, California.

Successful Trapping Methods. By Walter S. Chansler. D. Van Nostrand Company, Inc., New York. 1955. viii + 151pp. $3.95.

This book consists of 25 chapters which cover the many phases of trapping. It starts with three chapters on the often-neglected area of the trapping grounds and how to locate them. This is followed by three chapters on equipment and four chapters on a general discussion of trapping procedure. The eleventh through twenty-first chapters are concerned with the specific methods of taking the various fur bearers. The book ends with one chapter each on the care of skins, marketing, tanning furs, and trapping laws.

The several discussions on trapping fur bearers are good as far as they go and will be of help to the beginner but have little to offer the experienced trapper.

There is also considerable information on the biology and distribution of the fur-bearing species included. Unfortunately much of the data on present distribution and biology are incorrect. Such statements as "The weasel brings forth each year two or rarely three litters . . ." (p.61), "Its [red fox] weight is from thirty to thirty-five pounds" (p.97), "Like the raccoon, the animal [otter] often hibernates during cold weather . . ." (p.116), demonstrate a lack of accuracy since it has been shown that the weasel has but a single litter a year, that it takes a large fox to weigh 13 pounds, and that the otter does not hibernate. In general the statements on distribution are reasonably correct. However, such statements as the timber wolf ". . . inhabits the western parts of the United States and many parts of Canada" (p.13) are highly misleading. The author's concept of a species is not well founded as is shown by: "There are several other species of foxes [other than red and gray], including the Black Fox, the Kit Fox, the Swift Fox, the White Fox, the Blue Fox, and the Silver Fox." Only five of the eight forms listed represent species.

The book is well bound and printed on good paper. Its appearance is attractive and it is decorated with numerous pen sketches. While these sketches normally illustrate some trapping methods, they are not referred to in the text.

It is unfortunate that our recent knowledge of distribution and biology was not drawn into this book. As it is, I cannot recommend it for beginning or professional trappers.—JAMES R. BEER, Department of Entomology and Economic Zoology, University of Minnesota, St. Paul 1, Minnesota.

Wisconsin's Renewable Resources; A Report on Research at the University of Wisconsin. By James A. Larsen. Published by the University of Wisconsin, Madison. xiv + 160pp. 1956. Limited free distribution in paper- and cloth-bound copies.

"If there is a single theme running through this book, it is that research has done much to help solve many of the problems posed by the need to manage wisely and well the natural, renewable resources of Wisconsin."

The foregoing quotation comprises the first paragraph of the Introduction to this book. Yet the book itself is more than a review of Wisconsin's research accomplishments in the field of natural resource management.

Part I deals with the history and ecology of such basic resources as soil and vegetation. It reviews man's uses and abuses of land and its products, and concludes with a chapter on rural zoning.

Part II is concerned with wildlife, its primitive distribution and abundance, the effect of man and his activities on wildlife populations, and the history of his attempts to manage game birds and mammals. It includes chapters dealing with quail, pheasants, Hungarian partridge, prairie and sharptail grouse, waterfowl and whitetail deer. Advances in management techniques resulting from research are emphasized.

Part III considers water, particularly as it relates to fish populations and the aquatic organisms on which fish depend. Here, as in the case of wildlife, basic research on problems in aquatic biology has led to advances in lake and stream management for better fishing. Accomplishments as well as needs for further research are briefly reviewed.

The book is neither a text on game and fish management nor a technical report on results of individual research projects. It is, however, a readable and informative account of the conservation history of Wisconsin, with special emphasis on the role that research has played in furthering fish and wildlife abundance.—R. D. BURROUGHS, Michigan Department of Conservation.